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Effects of fire and treefalls on Japanese climbing fern and native species groundcover in a restored longleaf pine savanna

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EFFECTS OF FIRE AND TREEFALLS ON JAPANESE CLIMBING FERN AND NATIVE SPECIES GROUNDCOVER IN A RESTORED LONGLEAF PINE SAVANNA

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Abstract

Recurrent disturbances play an important role in maintaining longleaf pine savannas. Windstorms and fires contribute to the heterogeneity of pine savanna understory through generation of canopy gaps and fuel accumulation, distribution and consumption. The combination of windstorms and fires promotes native herbaceous species, but also promotes invasion of Japanese climbing fern (*Lygodium japonicum*). *Lygodium japonicum* is an invasive fern with subterranean rhizomes and copious spore production invading pine savannas along the southeastern Gulf Coast Region. This dissertation examines how fire, previous windstorm disturbances, and animal disruptions influence *L. japonicum* and native species abundance in a restored longleaf pine savanna. Studies were conducted at Girl Scout Camp Whispering Pines, an upland mesic site containing longleaf pine in Tangipahoa Parish, Louisiana. I experimentally examined *L. japonicum* response to various fire severities during prescribed fire by manipulating fine fuels in the understory. Three fine-fuel treatments (increased, reduction, unaltered) were applied to plots containing fern genets. The effect of fire severity through duration of heating was transient on frond emergence, suggesting that established fern genets survive subsequent fires. Native groundcover species abundance and composition was also transiently influenced by fire severity, as examined in a *post hoc* fuel manipulation study. Abundance and composition of native species within localized areas differed based on heterogeneity of fire severity, indicating sensitivity to prolonged heating. Heat released, a product of fuel accumulation, may stunt recovery of native groundcover in localized areas and contribute to understory patches susceptible to invasion by non-native species. Animal biopedturbations were strongly associated with stump locations, which provided refuge and foraging opportunities in the understory. Biopedturbations did not, however, promote or suppress *L. japonicum* frequency or density. Windstorms and fire disturbances contributed to heterogeneity of groundcover and, thus

influenced *L. japonicum* spread. Particular growth characteristics of *L. japonicum* enabled persistence in certain locations. Areas with open canopy, where fire severity was low, were at higher risk of invasion than areas under pine trees. Fire is essential for restoration, yet promotes invasion by *L. japonicum*. Careful consideration of disturbance regime and characteristics of invasive species are required for successful maintenance of longleaf pine savannas.

Chapter 1

Introduction

Savanna ecosystems are dependent on recurrent disturbances. Recurrent disturbances are integral to maintain these perennial grasslands, which cover approximately 20% of the globe (Andersen et al. 2005, Bond and Keeley 2005, Govender et al. 2006, Gurevitch et al. 2006, Masocha et al. 2011). Longleaf pine savannas are typical of other savannas, in that recurrent disturbances are important for maintaining structure and composition (Turner et al. 1997, Gilliam and Platt 1999, Brockway et al. 2006, Frost 2006, Walker and Silletti 2006). Pine savannas occur in the Gulf Coast region, from Florida to Texas, and northward into North Carolina and Virginia (Frost 1993, Platt 1999, Frost 2006). The structure of pine savannas typically consists of open, discontinuous overstory scattered with large pine trees and continuous, groundcover comprised of herbaceous vegetation and sparse woody shrubs (Brockway et al. 1998, Provencher et al. 2001). Longleaf pine savannas are also biologically diverse. Exclusion or suppression of disturbances within pine savannas can result in loss of biodiversity, invasion of non-native species, and encroachment of woody species (Harper 1913, Wahlenberg et al. 1939, Varner et al. 2005, Frost 2006, Mitchell et al. 2006). Loss of recurrent disturbance may result in conversion of a pine savanna to a hardwood forest.

Pine savannas are influenced by various types of disturbances. These disturbances can be abiotic or biotic. Abiotic disturbances include windstorms (e.g., hurricanes, thunderstorms), lightning strikes and fire. The occurrence of an abiotic disturbance may result in the creation of canopy gaps from winds snapping or tipping up trees, ignition of fuels in the understory or single tree kills from lightning strikes (McGuire et al. 2001, Platt et al. 2002, Gilliam et al. 2006, Mitchell et al. 2009). Biotic disturbances include animal-generated soil disturbances (biopedturbations) and insect outbreaks (Harrington 2006, Means 2006). Biopedturbations may lead to disruption of the seed bank and burial of existing vegetation, while insect outbreaks may

cause gap formation by killing trees. Both abiotic and biotic disturbances may alter the structure and species composition within a pine savanna.

Windstorms and fire are two important abiotic disturbances influencing pine savannas. The physiognomy of pine savannas is largely a result of these two large-scale disturbances (Gilliam et al. 2006). Windstorms maintain the discontinuous overstory (Platt et al. 1988b, Platt and Rathbun 1993, Platt et al. 2000) and fires influence the diverse groundcover (Mushinsky and Gibson 1974, Platt 1999, Peet 2006, Thaxton and Platt 2006, Pecot et al. 2007, Myers and Harms 2009a). Windstorm disturbances, such as hurricanes, generate canopy gaps (McGuire et al. 2001, Gagnon et al. 2007) and a non-uniform distribution of both coarse woody fuels (tree stumps, boles, and branches) and fine fuels (pine needles) in the understory. The intensity, frequency, and extent of windstorm disturbances translate into various degrees of canopy cover, which influence light levels and the heterogeneous accumulation and arrangement of fuels in the understory (Myers and van Lear 1998, McGuire et al. 2001, Pecot et al. 2007, Sah et al. 2010). Flammable fuels generated in various amounts influence fire spread through the understory and can lead to differences in fire behavior and fuel consumption (Thaxton and Platt 2006). Fire severity varies based on fuel accumulation, resulting in a patchy mosaic of herbaceous groundcover in the longleaf pine savanna (Brewer et al. 1996, Myers and van Lear 1998). Fire both consumes and promotes vegetation in the understory, thus perpetuating the cycle of disturbance. The combined interactions of windstorms and fires result in local variation of fire severity (Platt et al. 2002) and, thus yield favorable conditions for native vegetation in the longleaf pine savanna.

Frequent fires are necessary for the persistence of pine savannas. Fire historically returned on short-term intervals (1-5 years) by lightning strikes or indigenous peoples (Glitzenstein et al. 1995, Varner et al. 2005, Glitzenstein et al. 2012 and references within).

Longleaf pine savannas are reliant on frequent, low-intensity fires to increase resource availability and maintain the rich biodiversity of flora and fauna (Waldrop et al. 1992, Platt 1999, Moser and Yu 2003, Frost 2006). Fire plays the role of consumer and promoter, by removing flammable fuels in the understory and stimulating regeneration of vegetation. Ecosystem persistence is, thus, dependent on the presence of resinous, longleaf pine needles and herbaceous fine fuels for fire spread (Landers and Wade 1994).

Groundcover vegetation may be influenced by biopedturbations in the longleaf pine savanna. Biopedturbations are animal-generated soil disturbances (Whitford and Kay 1999, Eldridge et al. 2009), such as creation of shelter through burrowing and foraging. These activities may alter resource availability (Mazía et al. 2010), disrupt or damage existing plant species (Milton et al. 1997, Hooper et al. 2000, Otfinowski and Kenkel 2010), alter the physical and structural function of groundcover (Eldridge et al. 2009), and impede fire movement through fuel manipulation in the understory (Mazía et al. 2010, Carvalho et al. 2012). Recurrent biopedturbations may influence plant species composition by enhancing or hindering colonization and establishment.

Small-scale soil disturbances provide opportunities for plant colonization and establishment. Biopedturbations are small-scale (localized to few meters) disturbances that occur at high frequency and low intensity in the pine savanna (Hermann 1993, Simkin et al. 2001, Simkin and Michener 2005). Burrowing animals can influence plant composition (Platt 1975, Milton et al. 1997, Schiffman 1997, Hooper et al. 2000) through seed bank turnover and release of resources. In the longleaf pine savanna, animal disturbances may influence establishment of individual plant species in the continuous understory. For example, gopher tortoises disrupt soil during burrow construction, burying nearby vegetation while simultaneously releasing resources

for colonizing species (Hermann 1993, Guyer and Hermann 1997). Animal activity may also influence fire severity via fuel load manipulation, as has been documented with ants in tropical savannas (Carvalho et al. 2012). Burial of vegetation may impede fire movement and behavior resulting in increased patchiness of plant composition (Milton et al. 1997). Additionally, there may be an interaction between biopedturbations and previous windstorm disturbances. Animal activities that manipulate the soil surrounding tree falls, stumps, or tip-ups may modify plant species composition within the localized area (Means 2006). Areas of soil disruption may become hot-spots for plant colonization, supporting both native and invasive plant species (Whitford and Kay 1999, Mazía et al. 2010).

Habitat fragmentation and fire suppression have degraded the longleaf pine savanna ecosystem, altering plant composition. Once covering between 25-36 million hectares, only 2-3% of the longleaf pine savanna remains in the southeastern Gulf Coast Region (Frost 1993, Moser and Yu 2003, Frost 2006, Platt et al. 2006, Leichty et al. 2011a). Fire suppression has resulted in woody shrub encroachment and the displacement of native groundcover species (Croker and Boyer 1975, Platt 1999, Drewa et al. 2002, Frost 2006). Further, invasion by non-native species, such as Japanese climbing fern (*Lygodium japonicum*), has followed fire suppression (Chapter 1, Leichty et al. 2011a). Re-introduction of fire has, therefore, been widely considered important for restoration of structure and composition of fire-suppressed longleaf pine savannas (Gilliam and Platt 1999, Brockway et al. 2006, Frost 2006, Walker and Silletti 2006).

Restoration of fire is essential for rebuilding longleaf pine savannas. Re-introduction of fire into a fire suppressed ecosystem, however, requires clear goals. Typically, goals include re-establishment of native groundcover, maintenance of overstory pines, and reduction of woody

and non-native species (Varner et al. 2005), though specific species may drive management goals (Jones and Chamberlain 2004). Re-introduction of low-intensity prescribed fire that resemble historic lightning-ignited fires tend to promote herbaceous groundcover vegetation (Platt et al. 2006, Walker and Silletti 2006), while restricting woody species (Olson and Platt 1995, Drewa et al. 2002). Increased native groundcover generates a rise in heterogeneous accumulation of flammable fine-fuels and facilitates fire spread in the understory (Beckage et al. 2009, Gagnon et al. 2010). Variable fuel load leads to variable fire behavior which differentially influences patches in the understory. Variation in understory patches enhances species diversity, producing recruitment opportunities for many species with different colonization requirements (Brewer et al. 1996, Mitchell et al. 2006, Thaxton and Platt 2006). Re-establishment of fires that are heterogeneous in severity and effects at local scales should differentially affect vegetation during restoration and lead to high plant diversity in longleaf pine savanna groundcover (Mitchell et al. 2006, Hiers et al. 2009).

Disturbances vital to longleaf pine savanna persistence may also benefit non-native species. Disturbances have been recognized as facilitating invasive species (Hobbs and Mooney 1991, D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992, D'Antonio and Meyerson 2002, Setterfield et al. 2005, Martinson et al. 2008) by releasing resources in the ecosystem (Shea and Chesson 2002, Shea et al. 2004, Setterfield et al. 2005, Gundale et al. 2008). Recruitment opportunities can occur after fire, windstorms, and biopedturbations (Milton et al. 1997, Schiffman 1997, Pecot et al. 2007). The interaction between fire and windstorm disturbances can have combined influential effects on variable resource release in the understory, which contributes to groundcover composition through canopy gaps, increases in light availability, and fuel distribution and consumption (Haywood et al. 1998, Platt et al. 2002, Passmore 2005,

Gagnon and Platt 2008, Liu et al. 2008, Pederson et al. 2008). Biopedturbation may influence localized regions surrounding previous windstorm disturbances, releasing additional resources for colonization, while influencing fire behavior through fuel load alteration. The interactions of these disturbances may influence successful colonization and establishment within the plant community of the longleaf pine savanna and be particularly beneficial to invasion by those non-native species that can withstand the recurrent disturbances. Non-native species invading longleaf pine savannas should be examined for their ability to withstand and respond to multiple, interacting disturbances at different scales.

Ecology of *Lygodium japonicum*

Japanese climbing fern is an invasive fern with multiple means of reproduction and spread. Initial colonization results from copious, wind-dispersed spores (Munger 2005, Koop 2009, Minogue et al. 2010, Robinson et al. 2010), which readily germinate in moist, open patches of sterile soil, such as canopy gaps (Koop 2009, Robinson et al. 2010). Gametophytes are self-compatible (Lott et al. 2003, Koop 2009), increasing successful germination and establishment of a small founding population when arriving in suitable locations. Under ideal conditions, mature sporophytes develop subterranean rhizomes and aboveground fronds that grow indeterminately (Munger 2005, Van Loan 2006a, Koop 2009, Minogue et al. 2010). Mature sporophytes may continue to spread belowground by vegetative expansion or continuous spore production (Van Loan 2006a, Koop 2009). Fronds climb and twine neighboring plants, forming dense mats that smother native groundcover vegetation (Munger 2005, Minogue et al. 2010, Leichty et al. 2011a). Once established, *L. japonicum* genets may persist through recurrent disturbances and increase in size. As genets increase in size, production of spores increases, thus

creating a cycle of ever expanding invasion. The growth characteristics of *L. japonicum* aid in how particular disturbances affect colonization and establishment success (Huston 2004).

Description of Study Site

My dissertation research was conducted at Girl Scout Camp Whispering Pines, located in Tangipahoa Parish in eastern Louisiana (30^o 41' N; -90^o 29'W). This upland, rolling hills site contains mesic longleaf pine savanna and is situated on loess-capped fine soils (McDaniel 1990, Roth et al. 2008). Longleaf pines at the camp have a mean density of 293.3 no/ha $\pm$ 34.6 (mean $\pm$ s.e.), average diameter of 293.3 no/ha $\pm$ 34.6, and an average basal area of 293.3 no/ha $\pm$ 34.6 m^2/ha (Noel et al. 1998, Platt et al. 2006). During the past century, Camp Whispering Pines has experienced various land uses, including habitat fragmentation, logging, cattle grazing, and fire suppression (Platt et al. 2006, Leichty et al. 2011a). The overstory has remained relatively intact despite the different land uses and predominately contains longleaf pine (*Pinus palustris*) and high biodiversity groundcover vegetation dominated by bluestem grasses (e.g., *Schizachyrium scoparium* and *S. tenerum*) (Platt et al. 2006, Myers and Harms 2009a). Decades of fire suppression, however, resulted in increased abundances of woody shrubs, reduction of herbaceous groundcover, and invasion by non-native species including *L. japonicum* (Platt et al. 2006). The groundcover of Camp Whispering Pines has been influenced by the combination of windstorms, fire, and animal-generated soil disturbances, thus allowing for examination of the effects of combined disturbances.

Ecological restoration and management at Camp Whispering Pines was initiated in 1990 and has been ongoing for two decades. The restoration plan and management goals are described in Platt et al. (2006). Prescribed fires have been conducted biennially during the dry spring-wet summer transition (April-May) since 1992 (Platt et al. 2006, Leichty et al. 2011a). Low-intensity

fires, which burn in the understory, vary in local severity dependent on accumulation and arrangement of fuels distributed by windstorms, animal-generated disturbances, and distance from trees (Passmore 2005, Drewa et al. 2006, Platt et al. 2006, Thaxton and Platt 2006). Through these restoration efforts, a reduction of shrub abundance and an increase of herbaceous groundcover has been observed (Drewa et al. 2006, Platt et al. 2006, Thaxton and Platt 2006, Myers and Harms 2009a, Leichty et al. 2011a).

Objectives of Dissertation

My dissertation research explores the relationship between naturally occurring disturbances and groundcover vegetation in a restored pine savanna. Specifically, I examine the influence of fire severity on native and non-native species and investigate how groundcover composition is influenced by abiotic and biotic disturbances. The focal species of my research is *L. japonicum*. This species appears to be increasing in abundance at Camp Whispering Pines. Additionally, this invasive fern species and *Pteridium aquilinum*, a native fern that is tolerant of fire, have similar growth characteristics. Accordingly, I studied both native and invasive species, with emphasis on *L. japonicum*.

To address my objectives, I studied the effects of windstorms that produce tree stumps, prescribed fires being used in restoration, and ongoing biopedturbations on both native groundcover and Japanese climbing fern. I also focused specifically on how differences in fire severity associated with variable fuel accumulations influence native species composition and the abundance of *L. japonicum*. The results of my dissertation generated concepts regarding the invasion and spread of *L. japonicum* in light of current management actions that influence ongoing restoration of both Camp Whispering Pines and other longleaf pine savannas.

Dissertation Chapters

The chapters in this dissertation reflect separate studies examining how disturbances influence groundcover species composition in my site. Both Chapters 2 and 3 focus on fire as the primary disturbance and how groundcover vegetation is affected. Chapter 2 explores how frequent fire influences abundance of *L. japonicum* and how *L. japonicum* responds to different fire severities. Changes in *L. japonicum* abundance were assessed using two separate studies that focused on 1) the whole pine savanna and 2) patches in the groundcover with and without overstory trees. Different fire severities were generated through manipulation of fine-fuels (e.g., pine needle) surrounding fern genets. Chapter 3 is a *post hoc* examination of the effects of fire severity on composition of local assemblages of native species groundcover. Fire severity differences were generated by fine-fuel load manipulations, with total heat released calculated from total fuel consumption measures (Johnson and Miyanishi 1995). Chapter 4 is an observational study evaluating the combined effects of windstorm disturbances and biopedturbations on *L. japonicum* genet size and occurrence. Changes in animal-generated soil disturbances and *L. japonicum* near and away from tree stumps were censused to ascertain the advantages and disadvantages of colonization near disturbances. Chapter 5 summarizes the important results of the dissertation, examines management considerations and implications in light of the results, and suggests future research.

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Chapter Two

Response of Invasive Japanese Climbing Fern (*Lygodium japonicum*) to Prescribed Fire in a Restored Longleaf Pine Savanna

Introduction

Ferns occur in fire-frequented ecosystems worldwide. Some genera of ferns (e.g., *Adiantum, Asplenium, Blechnum, Dryopteris, Pellaea, Pteridium*) commonly occur as perennial sporophytes in the herbaceous groundcover of tropical/subtropical savanna ecosystems (Page 1976, 1979, Kornas 1993, Hemp 2002, Hietz 2010). Tropical/subtropical savannas, such as those in Africa (Govender et al. 2006), Australia (Whelan 1995, Clarke and Knox 2002), and the southeastern United States (Glitzenstein et al. 1995, Platt 1999, Slocum et al. 2010), typically experience strong seasonal wet/dry cycles and are subject to frequent, lightning-ignited fires. Ferns strongly associated with fire-prone ecosystems survive in ways similar to herbaceous perennial angiosperms in the same habitat. Growth characteristics, such as subterranean rhizomes that contain dormant buds and store nutrients for post-fire frond production (Kornas 1978, 1993, Mehltreter 2008), can improve survival. Bracken fern (*Pteridium aquilinum*), which is globally distributed (Gliessman 1978, Page 1986, Taylor 1986, Bray 1991, Engelman and Nyland 2006, Mehltreter et al. 2010, Robinson et al. 2010) can replace fronds from rhizomes in about one month post-fire (Alonso-Amelot and Rodulfo-Baechler 1996). An extensive spore bank (Engelman and Nyland 2006) and the ability to germinate in environments scarified by fire (Page 1976, Gliessman 1978) also aid colonization of open areas. As a result, bracken fern sometimes dominates post-fire assemblages (e.g. Rull 1999). These characteristics result in bracken fern being considered as a somewhat invasive fern, especially in fire-frequented ecosystems (Engelman and Nyland 2006, Schneider 2006, Schneider and Fernando 2010).

Non-native fern species with growth characteristics similar to invasive native ferns may be likely to invade fire-frequented ecosystems. Japanese climbing fern (*Lygodium japonicum*), native to temperate, subtropical and tropical regions of eastern and southeastern Asia and

northern Australia (Singh and Panigrahi 1984, Munger 2005, Van Loan 2006b, Willis et al. 2006, Mehltreter et al. 2010), is now invading longleaf pine savannas along the southeastern Gulf Coast (Leichty et al. 2011b). Rhizomes of this perennial fern indeterminately produce long, twining fronds (Clarke 1936, Mueller 1982, 1983, Van Loan 2006b) capable of copious production of spores, which germinate and mature in moist, open environments (Murtaza et al. 2004). Growth forms of *L. japonicum* sporophyte genets are similar to *P. aquilinum*, which is native to pine savannas (Page 1976, Gliessman 1978, Bray 1991, Engelman and Nyland 2006). Subsoil rhizomes of *P. aquilinum* survive fire (Gliessman 1978, Engelman and Nyland 2006, Walker and Sharpe 2010), and similar characteristics of *L. japonicum* thus may facilitate invasion of fire-frequented pine savannas.

Responses of ferns to fires appear to depend on the characteristics of fires. Some studies have indicated that portions of fern rhizomes are damaged when heat penetrates the soil (Flinn and Wein 1977, 1988). Thus, ferns with rhizomes located deeper in the soil should more likely recover (Page 1976, 1986, Hietz 2010, Walker and Sharpe 2010). Seasonal timing of fire also may affect post-fire regrowth (Preest and Cranswick 1978, Flinn and Pringle 1983). *Pteridium aquilinum*, for example, produces new fronds in the spring-early summer. If fires occur shortly after this new frond production, reductions in frond regeneration are expected because nutrient reserves are depleted (Preest and Cranswick 1978). Thus, severity of fires, in conjunction with seasonal timing, may influence both locations and dynamics of native and invasive fern populations in pine savannas.

In the current study, I address two questions regarding effects of fires on *L. japonicum*. First, does frequent low severity fire influence abundance of *L. japonicum*? This question was investigated at Camp Whispering Pines in eastern Louisiana using biennial growing-season

prescribed fires necessary for management of the native pine savanna (Drewa et al. 2006, Platt et al. 2006, Thaxton and Platt 2006, Myers and Harms 2009a, Leichty et al. 2011b). I anticipated that subterranean rhizomes of *L. japonicum* genets would survive typical growing-season fires because these fires would not generate heat necessary to damage the belowground structures. I further projected that established genets should recover quickly and produce spores that colonize new sites, resulting in increases in abundance as fires open space for colonization. I assessed changes in *L. japonicum* abundance in two separate field studies that focused on 1) the whole pine savanna, and 2) patches of groundcover with and without overstory trees.

Second, does variation in severity of fires affect survival of *L. japonicum* genets? Fire severity, the extent to which organic biomass is reduced by fire (Keeley et al. 2008, Keeley 2009), varies locally with amounts of flammable fuels (Johnson and Miyanishi 1995). In pine savannas, local variation in fuels change fuel consumption, maximum temperatures, and damage to groundcover plants (Thaxton and Platt 2006). Such differences in fire severity associated with localized fuel loads might influence post-fire frond production by ferns with shallow rhizomes. The plagiotrophic, horizontally extending rhizomes of *L. japonicum* are 1-3 cm belowground (Clarke 1936, Mueller 1982, Leichty et al. 2011b), compared to 15-30 cm for *P. aquilinum* rhizomes (Flinn and Wein 1977, Walker and Sharpe 2010). Thus, *L. japonicum* might be more sensitive to high fire severity than *P. aquilinum*.

To explore the second question, I conducted a field experiment to assess how variation in fire severity may influence fern rhizomes. I anticipated that decreased fuel loads (e.g., in the open away from pines (Platt et al. 1991)), should result in decreased fire severity and thus less damage to rhizomes. Reduced rhizome damage is expected to result in increased post-fire re-emergence of *L. japonicum* fronds, as well as larger genets present over time. Conversely,

increased fuel loads, (e.g., under pine trees (Platt et al. 1991)), should result in increased fire severity, more damage of rhizomes and thus, reduced post-fire fronds comprising *L. japonicum* genets. I conducted a field experiment in which I manipulated fuel loads in plots containing *L. japonicum* and measured persistence and re-emergence following prescribed fires. I used these data, along with data on changes in abundance over time, to characterize patterns of invasion of pine savannas at Camp Whispering Pines by Japanese climbing fern.

Methods

Field Site: I conducted two field studies and one field experiment at Girl Scout Camp Whispering Pines in Tangipahoa Parish in eastern Louisiana (30^o 41' N; -90^o 29' W). This upland, rolling hills site contains longleaf pine savanna situated on loess-capped fine sand soils (McDaniel 1990, Roth et al. 2008). Longleaf pines at the camp have a mean density of 293.3 no/ha $\pm$ 34.6 (mean $\pm$ s.e.), average diameter of 293.3 no/ha $\pm$ 34.6, and an average basal area of 293.3 no/ha $\pm$ 34.6 m^2/ha (Noel et al. 1998, Platt et al. 2006). Camp Whispering Pines has been influenced by habitat fragmentation, logging, open range grazing by cattle, and fire suppression (Platt et al. 2006, Leichty et al. 2011b). The overstory has remained relatively intact despite the different land uses and predominately contains longleaf pine (*Pinus palustris*) and high biodiversity groundcover vegetation dominated by bluestem grasses, such as *Schizachyrium scoparium* and *S. tenerum* (Platt et al. 2006, Myers and Harms 2009a). Ecological restoration and management at Camp Whispering Pines has involved prescribed fires conducted biennially during the spring-summer transition (April-May) since 1992 (Platt et al. 2006, Leichty et al. 2011b). After 20+ years of restoration, shrubs have been reduced in abundance, and herbaceous groundcover plants have increased (Platt et al. 2006, Thaxton and Platt 2006, Myers and Harms 2009a, Leichty et al. 2011b).

Prescribed fires at Camp Whispering Pines are constrained to seasonal timing dependent on local synoptic weather conditions. All fires occur following one-two weeks without rain during the transition from dry spring to wet summer conditions. For example, in 2007 all fires occurred in May, approximately 12 days after rain.

Three blocks were used within the total area to be burned. Two blocks were burned at different times on the same day and the third block was burned the following day. For both days, maximum air temperature was between 27-30 ^{O}C, average humidity was about 50%, and wind speeds were 11-16 km/hr with maximum gusts about 32 km/hr. Each block was ignited separately, with all plots burning as part of the larger fire. All fires burned across the blocks as flanking-head fires (in front of winds of 2.24-6.71 m/s) with flame lengths typically 0.5-2 m.

Field Studies of Spread of *L. japonicum*: I studied changes in abundance and sizes of Japanese climbing fern genets using two separate field studies. Plots for both field studies were carefully established to avoid soil disturbances. To assess changes across pine savannas at Camp Whispering Pines, I established 148 randomly located 1 m^2 circular plots in two blocks within several hundred hectares of longleaf pine savanna (field study 1). Any *L. japonicum* fronds rooted in each plot were counted before the 2006 fires. Abundance was calculated as the percentage of plots containing *L. japonicum* from the total plots sampled. Plots were sampled annually at the end of the growing season from 2006 through 2009. The two blocks experienced fire in the spring-summer transition of 2006 and 2008.

I also used data on *L. japonicum* from an ongoing long-term study of pine savanna groundcover to explore changes in abundance in specific microsites at Camp Whispering Pines (field study 2). Ten 1-hectare plots at Camp Whispering Pines were established by Noel et al. (1998) to study overstory pine dynamics. Establishment of these plots were based on the North

Carolina Vegetation Survey Protocol described by Peet et al. (1998). All pines in each plot had been mapped with an electronic total station. In 1996, 0.1 hectare patches within each plot were randomly selected for tree removal (Platt et al. 2006). Tenth-hectare patches selected had a continuous overstory of longleaf pine present, and resulting openings did not overlap edges of the 1 ha plot. Trees were cut at the base using chainsaws; boles and crowns were dragged from areas cleared using skidders. Attempts were made to minimize groundcover disturbance; this logging did not result in large differences in plant species composition in the groundcover (Platt et al. 2006).

In 2001, three locations in each plot were selected randomly using stratified sampling based on the condition of the overstory pines. First, a point was selected within the logged patch, subject to the restriction that it was in the open at least 10 m from the nearest living pine. A second random point was selected from patches that had been without an overstory for at least 30 years within each plot, again subject to the restriction that the point was at least 10 m from the nearest pine. Locations of the second point were based on aerial photography and records indicating that no logging had occurred within the area since 1920-1930. A third point was selected that had continuous cover of overstory pines within 10 m in all directions from the point. The three points were used as the center of 10 x 10 m (100 m^2) plots established in 2001 (Platt et al. 2006).

Each plot was sampled for Japanese climbing fern beginning in the fall of 2001. Subsequent sampling was conducted in the fall following biennial prescribed fires. Presence of *L. japonicum* was recorded in each plot sequentially, beginning in a 1 x 1 m nested subplot, proceeding to a 3.16 x 3.16 m nested subplot, and last in the 10 x 10 m plot. The relative abundances of *L. japonicum* were obtained by weighting occurrences in 1 x 1 m subplots by 100,

3.16 x 3.16 m subplots by 10, and 10 x 10 m plots by 1. The resulting weighted abundance estimated the percentage of 1 x 1 m subplots in each 10 x 10 m plot (100) that contained Japanese climbing fern.

Analyses of *L. japonicum* abundance for both field studies were conducted using PROC MEANS in SAS 9.1.3 (SAS 2003). Simple linear regression was used to capture trends; R-square values indicated strengths of the trends.

Field Experiment of Effects of Fire Severity on *L. japonicum*: I studied effects of variation in fire severity on Japanese climbing fern experimentally. Plots containing *Lygodium japonicum* were established in three different blocks at Camp Whispering Pines to assess how variation in fire severity affects genet size. Within each block, 18 plots (54 total), each containing a *L. japonicum* genet, were installed in the spring of May 2007. These circular 1 m^2 plots were centered on a fern genet and all fronds rooted within the plot were censused. Clusters of fronds comprising the genet within each plot were identified pre-fire and marked with metal tags. Fronds were censused less than one month prior to May 2007 fires and one, six, and 12 months post-fire.

One of three fine-fuel treatments was randomly applied to each plot. Fuel treatments simulated accumulations and reductions of fine fuels, as described in Thaxton and Platt (2006). For fine-fuel increase, dry longleaf pine needles were collected outside the fire block. A total of 1.2 kg of air-dry pine needles was distributed uniformly within each plot (a 2.6 m^2 area including the plot, plus a 30 cm buffer), resulting in increases in needle density of about 0.5 kg/m^2 (Thaxton and Platt 2006). Densities of pine needles used were based on data presented in Thaxton and Platt (2006) and represented amounts >1 standard deviation above the mean, but less than the maximum occurring naturally at Camp Whispering Pines (e.g., under dense pine

overstory or beneath fallen pine tree crowns). For fine-fuel reduction treatments, fine fuels were clipped and removed, then scattered well away from plots so as to not influence fire severity within plots. For unaltered treatments, fine-fuels were not disrupted. The fuels in unaltered plots represented natural variation of fine-fuels in the pine savanna at Camp Whispering Pines. Fine-fuel treatments were applied approximately two days before fire.

Table 2.1. *A priori* hypotheses (and hypothesized causes) for the field experiment exploring effects of fine-fuel manipulations on numbers of fronds in clones of Japanese climbing fern at Camp Whispering Pines.

Hypotheses for Contrasts	
Fuel Treatments	
Ho	Fuel treatments should not differ in their effects on *Lygodium japonicum* frond re-emergence.
Ha1	Effects of unaltered fine-fuel treatment should not differ from fine-fuel increase and reduction treatments (because fine-fuel treatments should produce positive and negative effects that cancel each other).
Ha2	Effects of fine-fuel increases should differ from effects of fine-fuel reduction (because increases in fine-fuels should result in decreases in frond numbers, while fine-fuel reduction plots should result in increases in frond numbers).
Census Times	
Ho	Frond numbers should not differ significantly over time.
Ha1	Pre-fire numbers of fronds should differ from immediate post-fire numbers of fronds (because fires should kill current meristems and possibly damage dormant buds on rhizomes, reducing the number of emerging fronds).
Ha2	Post-fire numbers of fronds should increase over time (because rhizomes will grow and produce new fronds).
Interaction	
Ho	There should be no significant differences between fuel treatments that change over the duration of the experiment.
Ha	Differences among fuel treatments observed immediately post-fire should decrease over time as rhizomes recover and produce new fronds

Fire severity was estimated by using measurements of fuel consumption. Loss of organic matter, the basis for estimating fire severity (Keeley et al. 2008, Keeley 2009), was estimated using fuel combustion samples collected within the 30 cm buffer zone of each plot to avoid disrupting the plot. Pre- and post-fire fine-fuels were clipped within a 10 cm^2 area, oven dried at

50^{o} C, and weighed to determine total fuel consumption per plot. Fuel consumption was converted to total heat released per unit area using methods described by Johnson and Miyanishi (1995). Differences in total heat released among fuel treatments provided estimates of fire severity.

Effects of fire severity on numbers of fronds of *L. japonicum* were assessed using orthogonal contrast comparisons and mixed model analysis. Orthogonal contrast statements were defined to compare *a priori* hypotheses regarding effects of fuel treatments, census times, and the interaction between treatments on frond numbers (Table 2.1). Mixed model analysis involved repeated measures of plots within fire blocks. Fuel treatment and census time were assumed to be fixed effects, with census time being a repeated measure of the same plants within plots. Random effects in the study include fire blocks and interactions among fixed effects and individual plots (nested effects). Pre-fire frond count was used as a covariate to account for differences in genet size among plots. The sampling unit for the study is frond number/plot. PROC MIXED in SAS 9.1.3 (SAS 2003) was used to examine effects of fuel treatments and census times with α=0.05. Orthogonal contrasts were constructed to test differences among fuel treatments, census time, and their interactions using contrast statements constructed in PROC MIXED. Natural log transformed data were normal.

Results

Spread of *L. japonicum*: Abundance of *L. japonicum* at Camp Whispering Pines increased during field study 1. Japanese climbing fern was present in only 16% of the plots located across all pine savanna in 2006. By 2009, *L. japonicum* was present in 28% of the plots (Figure 2.1). The increase averaged about 4% per year, indicating spread across the pine savanna landscape. Sizes of established genets also increased over the four-year period: mean densities of fronds

increased 4-5 fold over the period of the study (Figure 2.2). Maximum occurrences, as well as maximum genet sizes, occurred in 2008. The observed pattern of increase suggested that fires opened space for colonization and clonal expansion by *L. japonicum*.

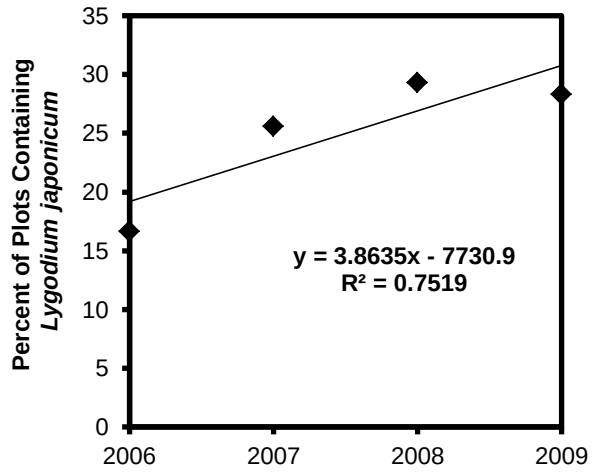

Figure 2.1. *Lygodium japonicum* occurrence over a four year period in restored longleaf pine savanna at Camp Whispering Pines. Data are expressed as the percentage of plots containing Japanese climbing fern and include the R^2 value.

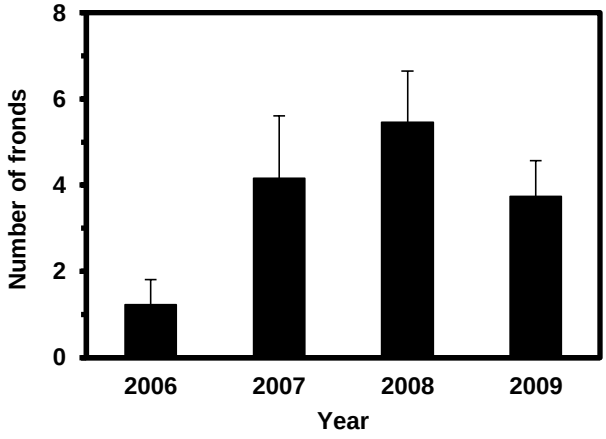

Figure 2.2. Sizes of genets of Japanese climbing fern over a four-year period during restoration of longleaf pine savanna at Camp Whispering Pines. Data are expressed as mean (± standard error) number of fronds per m^2.

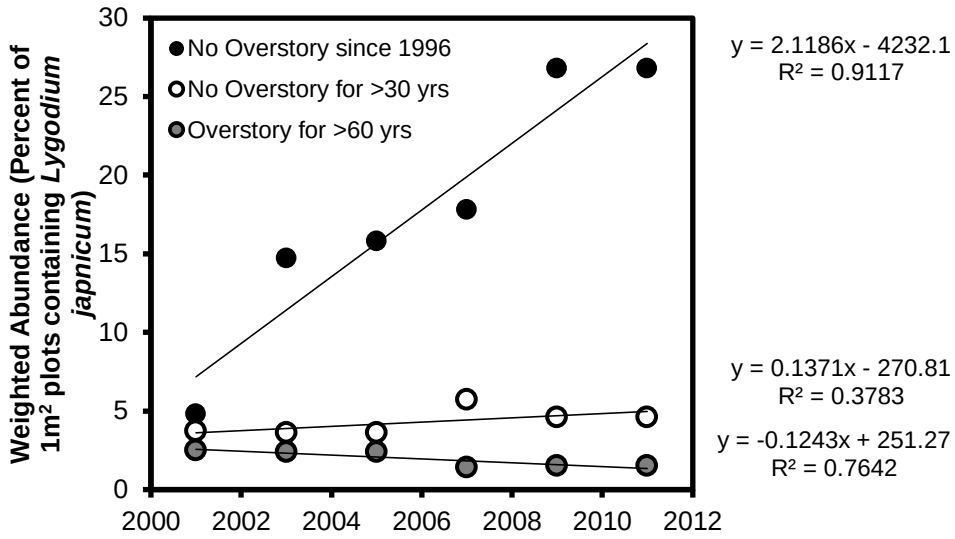

Figure 2.3. Changes in weighted abundance of *Lygodium japonicum* at Camp Whispering Pines over a ten year period. Plots were stratified by presence and absence of overstory pines and the length of times overstory pines had not been present. See text for further details.

Abundance of Japanese climbing fern at Camp Whispering Pines changed differently in areas with and without overstory pines (field study 2). Changes in weighted abundance of *L. japonicum* in the long-term groundcover plots are depicted in Figure 2.3. At the onset of measurements, *L. japonicum* was estimated to be present in less than 5% of the area comprising subplots, and abundances did not differ between locations with and without an overstory. Subsequently, abundance diverged in areas with and without a pine overstory during the field study. Abundance increased sharply in areas with no pine overstory since 1996, but decreased slowly in areas with a pine overstory for > 60 years. Increases of *L. japonicum* were considerably greater in subplots from which the overstory had been removed five years prior to the start of the study than in subplots that had contained no overstory for at least three decades (Platt et al. 2006). By 2011, weighted abundance in plots without an overstory since 1996 was more than 5 times that in plots without an overstory for > 30 years, indicating that invasion was proceeding at different rates in different area of Camp Whispering Pines.

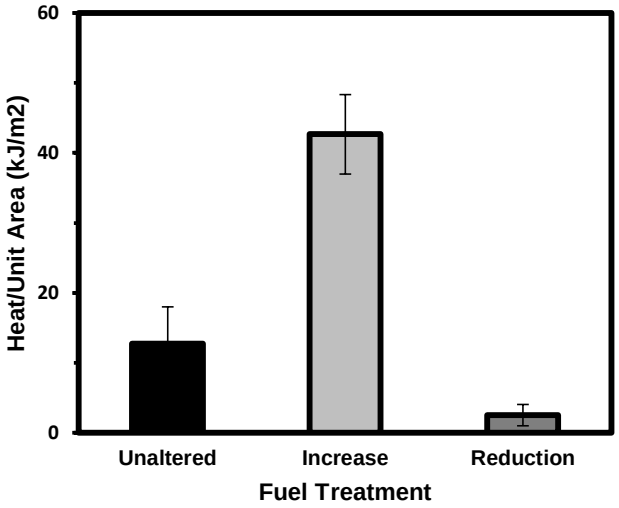

Figure 2.4. Total heat released per unit area for increased fuels, reduced fuels, and unaltered fuels. Total heat per unit area (kJ/m^2) was calculated by multiplying total fuel consumption (t/ha) by 18,800 kJ/kg (Johnson and Miyanishi 1995). Data are expressed as means $\pm$ standard errors.

Fire & Fire Characteristics: Fuel consumption was observed to differ among fuel treatments during the 2007 fires. Fires consumed the majority of aboveground fuels within the fine-fuel increase and unaltered fine-fuel plots. The presence of mostly white ash in fine-fuel increase plots indicated more complete fuel consumption than in unaltered plots, which contained less white ash. In contrast, fine-fuel reduction plots commonly contained some green, unburned fuels and fire movement was interrupted from traveling evenly across these plots. These differences among fuel treatments were confirmed by the data.

Heterogeneity in fuel consumption and fire spread was associated with differences in fuel consumption and total heat released generated by the fuel treatments. Total heat released per unit area (Figure 2.4) was significantly different among fuel treatments ($F=32.65$, $p<0.0001$, $n=54$). Heat released in unaltered plots was intermediate between heat released in fine-fuel increase and reduction plots. Total heat released during burning of fine-fuel increase plots was almost an

order of magnitude greater than total heat released in the fine-fuel reduction treatment (Figure 2.4).

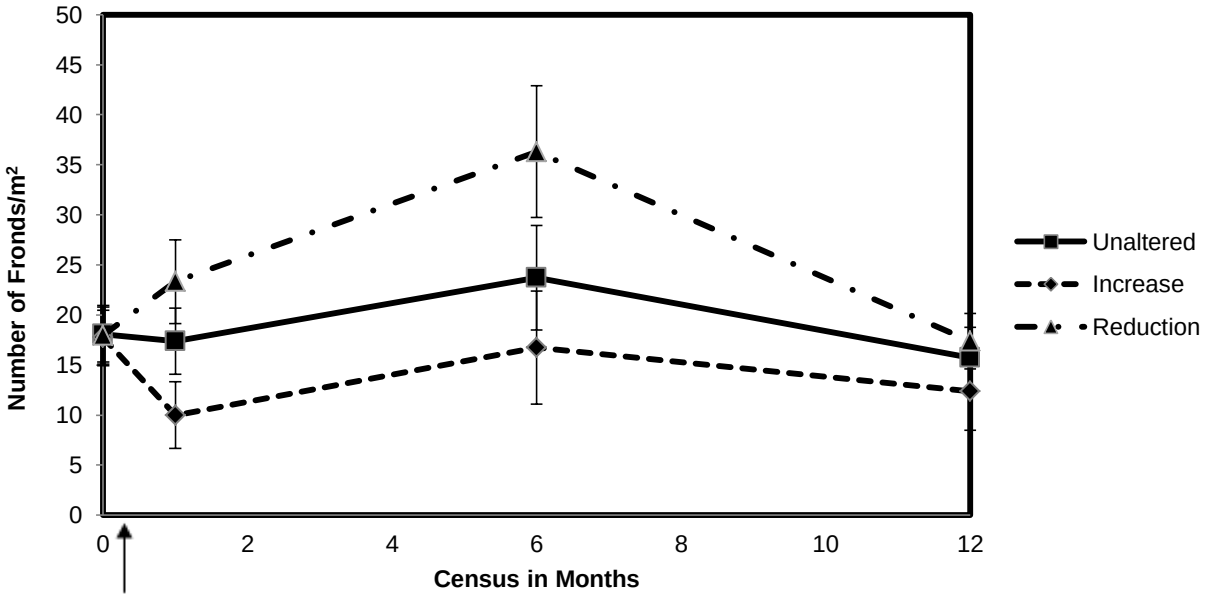

Figure 2.5. Effects of experimental treatments on genet size of *Lygodium japonicum* (number of fronds) over one year following prescribed fires in May, 2007. Frond numbers were censused pre-fire and one, six, and twelve months post-fire. Arrow indicates time of prescribed fire. Vertical bars indicate means $\pm$ standard errors.

Effects of Fuels on Size of *L. japonicum* Genets: Size of genets (numbers of fronds) was influenced by fuel treatment and sampling period (Figure 2.5). The pre-fire sizes of genets to which different treatments were applied were not significantly different. One-month post-fire, however, genet sizes had decreased in fine-fuel increase treatments and increased in fine-fuel reduction treatments, but remained similar in unaltered treatments. At six months, genets in all treatments had increased in size, but especially in fine-fuel reduction treatments. By twelve months, effects of fuel treatments on genet size were no longer apparent.

Table 2.2. ANOVA table displaying effects of fuel treatments, census times and their interaction on genet sizes of Japanese climbing fern. Natural log of pre-fire frond number was used as a covariate in the Proc Mixed analysis (SAS 2003). Fuel treatment denotes one of three fine-fuel treatments (unaltered, increase, reduction) applied to plots. Census refers to the time of census: pre-fire and one month, six months or 12 months post-fire. The AICC was 465.3 using AR(1) covariance structure in the REPEATED statement.

Type 3 Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Pre-fire Frond Number	1	160	97.67	<.0001
Fuel Treatment	2	6.11	4.11	0.07
Census	3	10.6	6.47	0.01
Fuel Treatment*Census	6	7.91	5.26	0.02

Table 2.3. Orthogonal contrasts comparing effects of fuel treatments (unaltered, increase, and reduction), census times (pre-fire, one, six, and 12 months post-fire), and the interaction between fuel treatment and census time on sizes of Japanese climbing fern genets. Orthogonal contrasts were established *a priori* to assess differences among fuel treatments, time of census, and the interaction between fuel treatment and census time. All statistical comparisons were conducted using SAS 9.1.3 denotes significant comparisons ($\alpha = 0.05$).

Contrasts				
Fuel Treatments	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Unaltered vs. Increase & Reduction	1	12.5	3.63	0.36
Increase vs. Reduction	1	12.9	11.67	0.03*
Census Time				
Pre-fire vs. All Post-fire Censuses	1	13	7.47	0.02*
6 months vs. 1 & 12 months post-fire	1	8.59	11.21	0.01*
1 month vs. 12 months post-fire	1	12.2	0.02	0.88
Interactions				
Unaltered/ Increase & Reduction vs. Pre/All Post-fire Censuses	1	16	3.37	0.09
Unaltered/ Increase & Reduction vs. 6 months/1 & 12 months	1	14.4	0.04	0.84
Unaltered/ Increase & Reduction vs. 1month/12 months	1	15.3	0.15	0.71
Increase/Reduction vs. Pre/All Post-fire Censuses	1	10.5	24.79	0.001*
Increase/Reduction vs. 6 months/1 & 12 months	1	5.01	0.33	0.59
Increase/Reduction vs. 1month/12 months	1	9.65	1.93	0.20

Comparisons of effects of fuel treatments on genet size illustrated in Figure 2.5 were supported by statistical analysis. Mixed model analysis indicated that fuel treatment did not result in significant effects on post-fire frond response (Table 2.2). These results were expected

because experimental fuel manipulations were within the natural range of fuel loads expected in the pine savanna and thus fire severity did not differ significantly among fuel treatments (cf. Thaxton and Platt 2006). Contrast analysis indicated no significant difference between numbers of fronds within plots in the unaltered fine-fuel treatment compared to both fine-fuel increase and reduction treatments (Table 2.3). Nonetheless, contrast analyses indicated large, significant differences between numbers of fronds within plots in fine-fuel increase and reduction treatments (Table 2.3). Thus, more extreme differences in localized fuels, such as those generated by the experimental treatments, influenced post-fire sizes of fern genets.

Time of census had a significant effect on the phenology of frond production. Mixed model analysis revealed that frond re-emergence was influenced by time since fire (Table 2.2). Numbers of fronds also differed significantly between pre-fire census and post-fire censuses (Table 2.3). Additionally, numbers of fronds per genet were significantly greater at the six-month post-fire census (end of the post-fire growing season) than the one-month and 12-month post-fire censuses. No significant difference in numbers of fronds was detected between one-month and 12-month post-fire censuses. These results suggest increases in fronds over the post-fire growing season, but that such increases may disappear by the following year.

Significant interactions also occurred between effects of fuel treatments and time since fire on sizes of genets of *L. japonicum*, as illustrated in Table 2.2. Strong interactive effects were evident when fuel manipulations (fine-fuel increase and fine-fuel reduction treatments) were compared for pre-fire relative to all post-fire censuses (Table 2.3). Effects of fine-fuel increase treatments were to decrease genet sizes over the year after fire, while effects of fine-fuel reduction were to increase genet sizes over the same period of time (Figure 2.5). Genet sizes in fuel-reduction plots had almost doubled over the post-fire growing season, in marked contrast to

the changes in genet sizes in unaltered or fine-fuel increase plots. Nonetheless, by one year after fire, there were no significant differences among treatments.

Discussion

The study demonstrates that rhizomatous ferns can invade fire-frequented savanna ecosystems. Frequent, low-intensity fires facilitate native herbaceous groundcover vegetation in pine savannas (Platt 1999, Platt et al. 2006, Walker and Silletti 2006), while concomitantly restricting cover and spread of woody species (Olson and Platt 1995, Drewa et al. 2002). These fires, while essential for management of this now-fragmented ecosystem, also potentially open habitat for invasion by other plant species. Grime (1979) predicted that plants with high reproductive rates should be those most likely to colonize disturbed habitats. Non-native *L. japonicum* is such a species, which has increased over time at Camp Whispering Pines.

Prolific production of spores may facilitate germination and establishment of *L. japonicum* in post-fire environments. Many ferns, including *L. japonicum*, produce wind-dispersed spores (Fletcher and Kirkwood 1979, Munger 2005, Engelman and Nyland 2006, Mehltreter et al. 2010). As a result, even if fire-scarified sites for germination and establishment occur intermittently, the "spore rain" (sensu Horvitz et al. 1998) could result in some spores immigrating onto local patches of soil following intense fire. Such sites, if moist, appear to be suitable for species with complex life cycles (e.g., Page 1976, Gliessman 1978). Moreover, some ferns, like *P. aquilinum*, even have a spore bank that survives low intensity fires (Fletcher and Kirkwood 1979). Additional research is needed to understand consequences of longevity and survival of fern spores, especially those produced by invasive species, in fire-frequented ecosystems like pine savannas.

Ferns that colonize pine savannas may encounter conditions that facilitate growth and maturation of gametophytes and sporophytes. Natural fires in longleaf pine savannas most often occur during the dry spring to wet summer transition, at times when thunderstorms produce lightning (Slocum et al. 2010). Post-fire environmental conditions at ground level, where spores are located, are likely to be warm and moist. Further, regrowth of groundcover plants that shade moist microsites should be conducive for germination, growth, and gamete exchange by fern gametophytes, as well as growth of sporophytes (Walker and Sharpe 2010). Such post-fire conditions are likely to be crucial for invasion by both native and non-native species with complex, alternating and free-existing life cycle stages.

Persistence of fern sporophytes after fires stems from subterranean rhizomes that produce new fronds from dormant buds. Rhizomes of ferns typically are persistent; for example, *P. aquilinum* rhizomes have been noted to remain viable for 35-72 years (Fletcher and Kirkwood 1979). Continuation of *L. japonicum* should be possible in a fire-frequented habitat if rhizomes exhibit similar viability of *P. aquilinum* and dormant buds are produced annually, as suggested following rapid frond production after clipping or fire (Evans et al. 2006, Minogue et al. 2010, Leichty et al. 2011b). The study indicated that once established, sporophyte genets of *L. japonicum* not only persist, but increased in size.

Survival of *L. japonicum* sporophytes may lead to continued invasion. Results of this study indicate that non-native ferns like *L. japonicum* can immigrate and become established in pine savannas, as well as survive frequent fires. Such species should naturalize, becoming a component of the already diverse groundcover and potentially contribute to high local groundcover biodiversity (e.g., Platt et al. 2006). This inherent ability to invade frequently

opened habitats like pine savannas raises questions about effects of frequent prescribed fires used in restoration on invading ferns like *L. japonicum*.

Rates of invasion should vary with local fuel conditions in pine savannas. The experimental study indicates that small-scale heterogeneity in fuels and resulting total heat released during fires (Hiers et al. 2009) influences post-fire frond production by *L. japonicum* genets. More fine-fuels decrease the emergence of fronds, most likely because it resulted in greater penetration of heat into the soil, which may damage or kill rhizomes. In contrast, reduction of fine-fuels result in increased emergence of fronds, suggesting less heat penetration and damage to subterranean rhizomes. Thus, *L. japonicum* rhizomes, only a few centimeters below the ground surface, are not completely insulated from heating in frequent fires. Rhizomes of *L. japonicum* should be more sensitive to local variation in fuel loads than those of *P. aquilinum*, which are not as close to the ground surface (Page 1976, 1986, Hietz 2010, Walker and Sharpe 2010).

Local heating variation appears to transiently affect *L. japonicum* frond emergence. Despite significant effects of altering local fine fuel loads on post-fire frond production, numbers of fronds in genets returned close to pre-fire numbers one year later. These data suggest that *L. japonicum* genets are likely to persist when fires occur frequently and are of low intensity. Increases in abundance and size of *L. japonicum* genets over the study period also support this hypothesis. Invasion of fire-frequented habitats by *L. japonicum* might be more likely than invasion by ferns with heat-sensitive rhizomes at similar soil depths (see Mehltreter et al. 2010). Lengthening fire regimes might increase fuel loads, thus slowing colonization and reducing genet size of *L. japonicum* through rhizome damage. Attempts to control *L. japonicum* by lengthening fire return intervals, however, also would likely have negative effects on native

species, reducing groundcover biodiversity. Thus there might be potential conflicts between managing biodiversity and managing for invasions of *L. japonicum* in southeastern pine savannas.

Effects of fuels on *L. japonicum* frond production raise questions about invasibility of different types of patches that naturally comprise pine savannas. Patch types in pine savannas associated with trees (Platt et al. 1988b, Noel et al. 1998, Gilliam et al. 2006) are also associated with local differences in fuels and variable fire effects (Thaxton and Platt 2006). Although the fuel manipulations were within the natural range of fuel accumulation in the longleaf pine savanna studied, fuel increases approached more extreme natural fine-fuel loads, such as those occurring under pine overstory trees. Indeed, the ten-year study indicated slow declines in abundance of *L. japonicum* beneath overstory pines, suggesting that this species should occur primarily in the open, away from pines at Camp Whispering Pines. Such patterns of fuel accumulation and spread suggest local differences in the distribution of *L. japonicum* and *P. aquilinum*. Genets of the non-native species should tend to occur in open treeless areas and away from pines, while genets of the native species, with deeper rhizomes, might be expected both in open areas and beneath trees. The other native fern common in upland pine savanna at Camp Whispering Pines, *Botrychium biternatum*, also occurs almost exclusively in open areas away from pine overstory (W. J. Platt, unpublished data); this species has rhizomes close to the ground surface, and may be more susceptible to severe fires as a result of heat sensitivity. These considerations of local distribution of ferns produce results consistent with the hypotheses of Gagnon et al. (2010) regarding effects of flammable fuels on species in fire-frequented habitats.

Location of fine fuels may dictate colonization and abundance of *L. japonicum*. Prescribed fire is important for ecological management of many southeastern ecosystems

(Roberts 1998, Pemberton et al. 2002). Under the current biennial prescribed fire plan, Japanese climbing fern is increasing, and more so in areas where overstory is absent. Areas without overstory tend to have decreased fuel load and thus, reduced fire severity, which benefit *L. japonicum* establishment. Reinstitution of biennial prescribed fire within longleaf pine savanna at Camp Whispering Pines has resulted in local increases in numbers of native species (Platt et al. 2006, Thaxton and Platt 2006, Myers and Harms 2009a, Leichty et al. 2011b), along with increases in *L. japonicum*. Both native herbaceous species and the invasive fern may well co-occur under the biennial prescribed fire regimes in this restored pine savanna.

Management of *L. japonicum* must focus on invasion of recently opened canopy locations. In areas of overstory canopy, *L. japonicum* slowly declines. Such declines would be expected to continue in both the short-term (between biennial fire return), as well as over the long-term (>60 years), because of increased fuel accumulation produced by overstory pines. Locations without canopy cover respond differently dependent on the time overstory has been absent. Recently opened canopy may result in a rapid increase of *L. japonicum* abundance, as seen in locations without overstory since 1996, because of reduced competition from native groundcover vegetation and increase resource availability. Longleaf pines seeds may simultaneously germinate and establish in these open areas where soil is exposed (Platt 1999, Harrington 2006). Japanese climbing fern abundance may slow as longleaf pines bolt from the grass stage toward mid-canopy and native species encroach in the open location (Platt 1999). It is, however, the transient period of no overstory that makes the pine savanna vulnerable to *L. japonicum* invasion. Susceptibility to *L. japonicum* invasion may result when overstory is altered from both natural (e.g., hurricanes, windstorms) and mechanical (e.g., logging) causes. Where new pine overstory develops (Gilliam et al. 2006), increases in fine fuels should result in

declines in the abundance of *L. japonicum*. In this context, *L. japonicum* may be on the way to becoming a component of the herbaceous groundcover.

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Chapter 3

Effects of Fire Severity on Native Pine Savanna Groundcover in a Restored Longleaf Pine Savanna

Introduction

Recurrent fires play a key role in many savanna ecosystems. Fires increase availability of resources (i.e., open space, increase light levels, release nutrients) and reduce competition by removal of aboveground biomass (Bond and van Wilgen 1996, Zedler 2007) in savannas in the southeastern United States (e.g., Platt 1999), Africa (e.g., Govender et al. 2006), and Australia (e.g., Whelan 1995, Clarke and Knox 2002). Many native species in these habitats tolerate, even benefit from fire disturbance, whereas other species may be reduced in abundance or eliminated (Bond and Keeley 2005). For example, longleaf pine savannas are biologically diverse ecosystems (Peet 2006) in which frequent fires facilitate savanna trees and herbaceous groundcover vegetation (Platt et al. 1988a, Moser and Yu 2003, Platt et al. 2006), while suppressing hardwood trees and shrubs (Glitzenstein et al. 1995). As a result, fire is integral in shaping the composition and structure of these ecosystems (Govender et al. 2006, Gagnon et al. 2010).

Composition and structure of fire-frequented ecosystems have changed around the world. Fire regimes have been altered, most often by human fire suppression (e.g., Bond et al. 2005, Bowman et al. 2009), which may result in compositional and structural changes in plant communities. Fire suppression in longleaf pine savannas has long been recognized to result in woody shrub encroachment and displacement of native groundcover species (Croker and Boyer 1975, Platt 1999, Drewa et al. 2002, Frost 2006). As a result, re-introduction of fire has been widely considered important for restoration of structure and composition of fire-suppressed longleaf pine savanna (Gilliam and Platt 1999, Brockway et al. 2006, Frost 2006, Walker and Silletti 2006).

Prescribed fire that mimics naturally occurring lightning fires is essential for restoration of southeastern pine savannas. Re-introduction of prescribed fires that resemble natural fires tends to restrict cover and spread of woody species (Olson and Platt 1995, Drewa et al. 2002), promoting herbaceous groundcover vegetation (Platt et al. 2006, Walker and Silletti 2006). The return of frequent, low-intensity fires enhances diverse native groundcover vegetation, which in turn promotes fire spread via accumulation of flammable fine-fuels (Beckage et al. 2009, Gagnon et al. 2010), facilitating the restoration of a fire-dependent ecosystem. Nonetheless, these fires are heterogeneous at local scales in their characteristics and effects (e.g.,Thaxton and Platt 2006, Hiers et al. 2009). Prescribed fires that are heterogeneous in their severity and effects, thus may differentially affect vegetation during restoration.

Fuels present in a localized area can influence fire severity. Fire severity describes the extent to which organic biomass is removed by fire (Keeley et al. 2008, Keeley 2009). Dependent on the local accumulation of flammable fuels (Johnson and Miyanishi 1995), fire severity can vary in extent as a result of continuous, yet heterogeneous fuel distribution (Brewer et al. 1996). In pine savannas, fine-fuels (i.e., pine needles) accumulate beneath trees and decrease in abundance as distance from the trunk increases (Thaxton and Platt 2006). Further, windstorms may result in addition of fine-fuels in localized areas; such increases in fine-fuels may result in localized areas where fires burn more severely (Passmore 2009), such as beneath overstory pines or downed tree crowns. In areas with greater fuel load, fire is likely to produce hotter temperatures and longer residence times at ground level. For instance, “hot-spots” from locally intense fires can damage belowground reproductive structures of resident species, resulting in a patchy mosaic of herbaceous groundcover in longleaf pine savannas (Brewer et al. 1996). Such local variation in fires potentially can influence changes in the composition and

structure of vegetation in the post-fire environment during restoration (Glitzenstein et al. 1995 and references within).

The influence of fire severity on native groundcover species may also vary dependent on locations of seeds or perennating organs. Native groundcover species within the longleaf pine savanna include annuals with soil seed banks and perennials with belowground rhizomes or roots. Damage of seeds and perennating structures close to the soil surface may occur if high temperatures and/or prolonged residence times, resulting from flammable fuels, generate high local fire severity. As a result, local areas of high fire severity should have decreased numbers of species compared to low fire severity locations. Local high fire severity also may be followed by changes in species composition if the site is opened for possible invasion by outside species or germination of dormant seeds. Shifts in plant species dominance may result in areas of high fire severity in the pine savanna.

I explored effects of differences in fire severity on the native plant species composition of the pine savanna groundcover in a restored longleaf pine savanna. I examined changes in species composition following prescribed fires in a study of the effects of differences in fine fuels on an invasive fern, *Lygodium japonicum* (Chapter 2). I conducted a *post hoc* analysis relating differences in total heat released among fine-fuel treatments during experimental fires to local composition and abundance of groundcover plant species over a 24-month period. I hypothesized that variation in fire severity associated with fine fuel accumulations should result in differences in native groundcover composition based on the total heat released in the localized area.

Methods

Field Site: The field study was conducted at Girl Scout Camp Whispering Pines, an upland mesic site that contains longleaf pine savanna in Tangipahoa Parish in eastern Louisiana. During the past century, Camp Whispering Pines has experienced different land uses, including habitat fragmentation, logging, open range cattle grazing, and fire suppression (Platt et al. 2006, Leichty et al. 2011b). The overstory has remained relatively intact and predominately contains longleaf pine (*Pinus palustris*) and high biodiversity groundcover vegetation dominated by bluestem grasses, such as *Schizachyrium scoparium* and *S. tenerum* (Platt et al. 2006, Myers and Harms 2009a). Nonetheless, decades of fire suppression resulted in increased abundance of woody shrubs, as well as reduced herbaceous groundcover (Passmore 2005, Thaxton and Platt 2006).

Ecological restoration at Camp Whispering Pines was initiated in 1990 and is ongoing after two decades. Platt et al. (2006) provide a general description of the goals and methodology employed as part of the restoration and management plan. Prescribed fires have been conducted biennially during the spring-summer transition (April-May) since 1992 (Platt et al. 2006, Leichty et al. 2011b). Fires burn in the groundcover and vary in local severity because fuel accumulation and arrangement are dependent on windstorms, disturbances, and distance from pine trees (Passmore 2005, Drewa et al. 2006, Thaxton and Platt 2006, Leichty et al. 2011b). Over the 20 years of restoration, shrubs have been reduced in abundance and herbaceous groundcover plants have increased in the upland pine savanna (Drewa et al. 2006, Platt et al. 2006, Thaxton and Platt 2006, Myers and Harms 2009a, Leichty et al. 2011b).

Prescribed fires at Camp Whispering Pines are constrained to seasonal timing that depends on local synoptic weather conditions. All fires occur following one-two weeks without

rain during the transition from dry spring to wet summer conditions. For this study, all fires occurred in May 2007, approximately 12 days after rain.

Three blocks were selected within the location to be burned. Two blocks were burned at different times on the same day and the third block was burned the following day. For both days, maximum air temperature was between 27-30 ^{o}C, average humidity about 50%, and wind speeds were 11-16 km/hr with maximum gusts about 32 km/hr. Ignition of fires for each block occurred separately, with all plots in each block burning as part of the larger fire. All fires burned across the sites as flanking-head fires (in front of winds of 2.24-6.71 m/s) with flame lengths typically 0.5-2 m.

Fire Severity Study: I experimentally examined the effects of variation in fire severity on pine savanna groundcover. Prior to prescribed fires in May 2007, 18 plots were randomly established in each of the three fire blocks (54 total plots); locations of plots were constrained to contain one genet of *Lygodium japonicum* (Chapter 2). Each circular plot was 1 m^2, with a 30 cm buffer to eliminate edge effects. Plots were randomly assigned to one of three fine-fuel treatments. These treatments were designed to simulate accumulations and reductions, as described by Thaxton and Platt (2006). Fine-fuel increase treatments represent >1 standard deviation above the mean pine needle density typically present in the pine savanna, yet remain under the maximum amount naturally occurring at Camp Whispering Pines. A total of 1.2 kg of air-dried pine needles was uniformly distributed within the plot, plus the buffer zone (a 2.6 m^2 area), resulting in increased needle density of approximately 0.5 kg/m^2 (Thaxton and Platt 2006). Fine fuels in the reduction treatments were clipped and removed, then scattered at least 5 meters away from plots to not influence fire severity within the study area. For unaltered treatments, fine fuels were not disrupted. The fuels in unaltered treatments represented the natural range of fine-fuel

accumulation found in the pine savanna at Camp Whispering Pines. All fine-fuel treatments were applied approximately two days prior to prescribed fires.

Fuel accumulations within plots were manipulated to generate differences in total heat released and to assess the influence of fire severity on groundcover vegetation. I calculated total heat released by measuring fine fuels pre- and post-fire. By measuring fine fuels before and after fire, I was able to determine total fuel consumption, which provided a convenient way to address whether native groundcover species are influenced by fire severity. Total heat released was obtained by calculating heat per unit area from the fuel combustion measurements using methods described by Johnson and Miyanishi (1995). The amount of fuel consumed in a given location provided a measure of fire severity, which indicated the extent of organic biomass removed by fire (Keeley et al. 2008, Keeley 2009). Pre-fire fuel combustion samples were collected within the 30 cm buffer zone 1-2 days prior to prescribed fires to avoid disrupting vegetation within plots. Post-fire fuel combustion samples were collected within the buffer zone a few hours after prescribed fires were complete. All samples were oven dried at 50^{o} C and weighed to determine total fuel consumed per plot. Most estimates of total heat released in fires were positive, although a few estimates were negative as a result of more fuel accumulation in the post-fire environment (e.g., wind-dispersed pine needles from canopy trees). Total heat released for each fine-fuel treatment was compared to estimate differences in fire severity.

Fire severity effects on native groundcover species were examined *post hoc*. Native groundcover species composition was sampled one, six, 12 and 24 months post-fire. In each plot, all plants were identified to species and categorized with respect to plant type (forb, graminoid, woody) and duration of life cycle classification (annual, annual/short-lived perennial, perennial). Graminoids contained species in *Cyperaceae* and *Poaceae*; forbs consisted of other herbaceous

species and ferns; and woody species included hardwood shrubs and vines. Stem counts were recorded for all species in each plot to estimate abundance of native species. A total of 148 species were recorded over the duration of the study. Data for the six-month post-fire census were not available from 7 plots. One plot was destroyed during salvaging operations after Hurricane Gustav and so no data were obtained from that plot in the 24-month census.

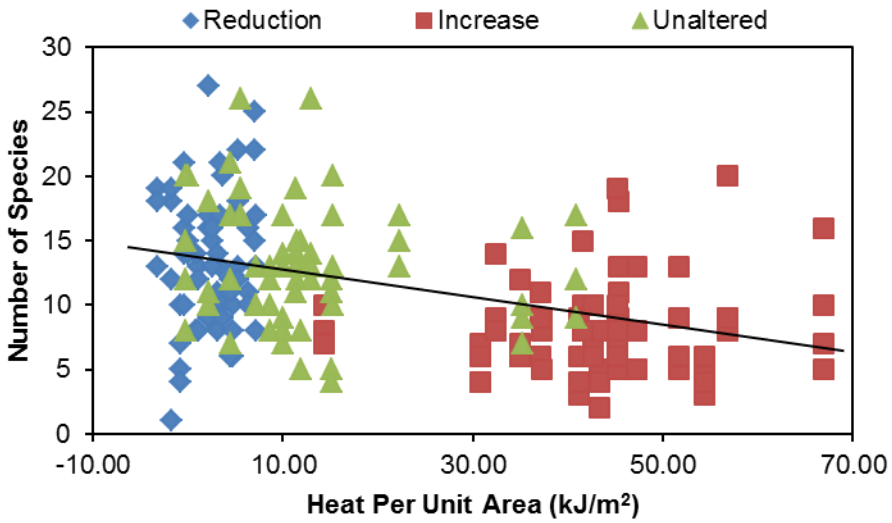

Figure 3.1. The relationship between the number of species in 1 m^2 plots and total heat released for three fine-fuel treatments (reduction, increase, and unaltered) in a 24-month period. Plots were sampled at four census times (one, six, 12, and 24 months). Prescribed fires occurred in May 2007 at Camp Whispering Pines, Louisiana. The solid line represents the estimated fit produced by linear regression ($y = 13.5 + (-0.10)\ x$, $R^2 = 0.17$).

The relationship between total heat released for all fuel treatments and number of species/plot was explored graphically across a 24-month post-fire period. As illustrated in Figure 3.1, plots clustered within two distinct ranges of total heat released. Group 1 (hereafter low fire severity) consisted primarily of plots in unaltered and reduction fine-fuel treatments, with fire severities ranging between -3.3 kJ/m^2 and 22.3 kJ/m^2. Group 2 (hereafter high fire severity) consisted primarily of plots in the fine-fuel increase treatment, with fire severities between 30.7

kJ/m^2 and 66.9 kJ/m^2. These groupings were related to fine-fuel treatments. Low fire severity included all fine-fuel reduction treatment plots, all but seven unaltered fuel treatment plots, and three fine-fuel increase treatment plots. High fire severity compromised all fine-fuel increase treatment plots, except for the three plots included in the low fire severity and the seven unaltered fuel treatment plots.

The two groups were used to draw comparisons and conclusions about fire severity effects. Total heat released was averaged for each group to compare differences in fire severity. Additionally, native species, by plant type and life form, were averaged by fire severity group for each post-fire census to examine effects to groundcover vegetation associated with fire severity.

Species Composition and Abundance Analyses: Statistical analyses were conducted using procedures in SAS 9.1.3 (SAS 2003). Proc Means and Proc Mixed were used to obtain basic statistics and to perform mixed model analyses. For all mixed model analyses, the compound symmetric covariance structure (CS) was used in the Repeated statement and *L. japonicum* abundance was used as a covariate because it was present in all plots. Normality of the data was determined using Proc Univariate (SAS 2003).

Multivariate analyses were conducted using Primer v6 with PERMANOVA+ add-on to explore differences in native species composition and abundance between fire severity groups (Clarke and Gorley 2006, Anderson et al. 2008). Data used for the Primer analyses was either square-root transformed to balance the contributions between dominant and rare species within the community or presence/absence transformed to determine which species were contributing to differences between fire severity groups. Species occurring once during the duration of the study were removed for all analyses. Bray-Curtis similarities of native species stem counts were used

to perform all ordinations. *Lygodium japonicum* was used as a covariate for all Primer v6 analyses.

Statistical hypothesis-testing was performed using distance-based linear model analysis (DistLM). DistLM, a permutation based, non-parametric method for multivariate regression analysis (Anderson et al. 2008), was used to explore how factors, such as fire severity group, total heat released, and time since fire, contribute to native species composition and abundance. McArdle and Anderson (2001) provide an explanation of the theoretical background of DistLM analysis. The DistLM routine was used in combination with distance-based redundancy analysis (dbRDA) ordination to visualize the multivariate relationships graphically (Anderson et al. 2008). Bray-Curtis similarities of native species stem counts were used to perform all ordinations. The step-wise selection procedure, with an AIC score, was used to determine the best model. The permutation number was set to 9999, as recommended by Anderson et al. (2008). Ordination analysis (dbRDA) was performed to determine patterns in species abundance and composition based on total heat released among fire severity groups at each census time.

Analysis of similarities (ANOSIM) and similarity percentage (SIMPER) procedures were used to determine if differences in species composition were present between fire severity groups and which individual species contributed to these differences. The ANOSIM procedure is similar to analysis of variance and was used to determine if species composition was significantly different between fire severity groups by producing an *R* statistic. The number of permutations was set to 10000 for the ANOSIM procedure. The SIMPER analysis is used once a significant difference is determined by ANOSIM.

SIMPER analysis was used to distinguish which native species contributed the most to differences detected by ANOSIM between low and high fire severity groups with the Bray-

Curtis similarity resemblance. I examined all species contributing 70% to the differences between fire severity groups. The SIMPER analysis also allowed for comparison of contribution by an individual species to differences detected between fire severity groups. From this list, species were selected for further examination. Selection of species was based on overall contribution to differences between fire severity groups, plant type, and life cycle classification. Additionally, some species were included because they only occurred in one of the fire severity groups. Non-metric multidimensional scaling (MDS) (Clarke and Gorley 2006) ordination plots were used to show patterns in abundance between fire severity groups at each census time for specific native species, plant types, and life cycle classifications indicated by the SIMPER analyses. Community data were averaged by fire severity group and census time for ease in illustrating differences in species abundance. The MDS analysis was performed using Bray-Curtis similarity index with 999 permutations. Native species abundance data was used to explore changes over time by fire severity group.

Results

Total heat released varied significantly among the fine-fuel treatments. Total heat released in the fine-fuel increase treatment averaged 43.3 $\pm$ 1.3 kJ/m^2 (mean $\pm$ 1 s.e., n=69), approximately 14 times greater than in the fine-fuel reduction treatment (2.6 $\pm$ 0.4 kJ/m^2, n=69). Total heat released in fine-fuel unaltered treatments was slightly greater than fine-fuel reduction treatments, with an average of 12.8 $\pm$ 1.3 kJ/m^2 (n=64). Mixed model analysis also indicated a significant difference in total heat released among fine-fuel treatments ($F_{2, 3.9}$= 398.7, p <0.0001). Variation in total heat released among fine-fuel treatments should lead to variation in fire severity, thus generating differences in number of species among fuel manipulations.

Differences in total heat released were reflected in number of species present in plots over a 24-month post-fire period. The *post hoc* comparison of the number of species in 1 m^2 plots and total heat released for fine-fuel treatments is presented in Figure 3.1. Total heat released in the low fire severity group (predominately fine-fuel reduction and unaltered treatment plots) was approximately 7 times greater than heat released in the high fire severity group (predominately fine-fuel increase treatment plots). Further, species number shows a slight decrease between fire severity groups, with a greater number of species present in the low fire severity group. Mixed model analysis detected a significant association of total heat released ($F_{1, 48.6}$ =23.4, p <.0001) and census time ($F_{3, 21.2}$ =37.3, p <.0001) with native species abundance. There was no significant interaction between degree of total heat released and time of census ($F_{3, 138}$ =0.5, p =0.68), indicating that numbers of native species did not change differently over time in low and high fire severity plots.

The relationship between fire severity and number of species was similar for graminoids, forbs, and woody plants. Locations experiencing less heating were associated with increased abundance of all plant types (Figure 3.2). Low fire severity graminoids and forbs had significantly greater species richness/m^2 than graminoids and forbs in high fire severity plots (Figure 3.2). Woody plant abundance was significantly greater in low fire severity groups than high fire severity groups, except at the six-month census. Further, SIMPER analysis showed that graminoid species (22.75%), forbs (31.70%) and woody (19.77%) species all contributed to the dissimilarity between fire severity groups. Mixed model analysis supported the relationship between fire severity and census time for all three native plant types (Table 3.1). The mixed model analysis did not, however, detect any significant effects of interaction between fire severity group and census.

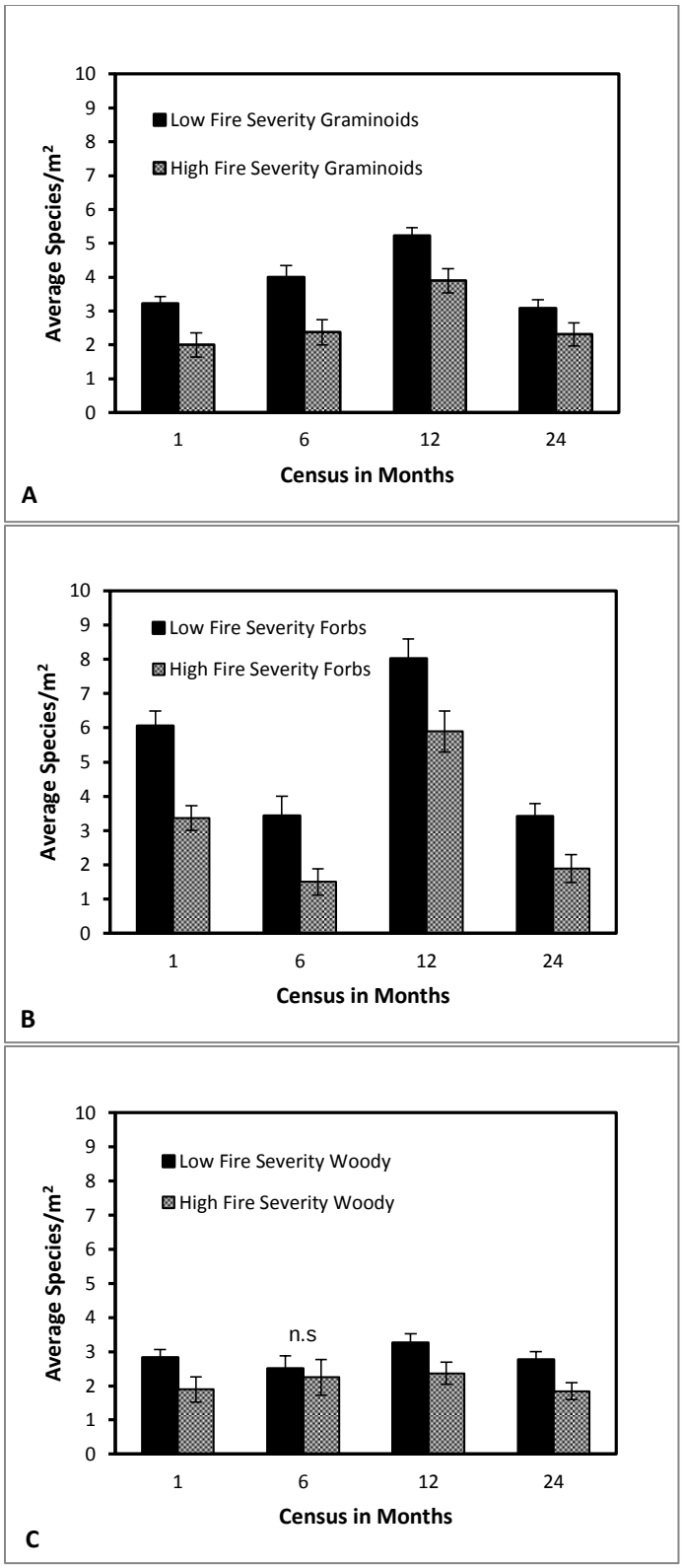

Figure 3.2. Changes in species abundance for low and high fire severity groups over two years following prescribed fires. Native species were placed in one of three categories: A) Graminoids B) Forbs C) Woody. Data are expressed as mean species number/m^2 $\pm$ standard errors.

Table 3.1. ANOVA table displaying effects of fire severity group, census, and their interaction for native groundcover species plant types. Group denotes one of two fire severities (low or high). Census refers to the time of census: one month, six months, 12 months, or 24 months post-fire. Proc Mixed analysis with CS covariance structure in the REPEATED statement was used to determine the model best fitting the data. An asterisk (*) indicated significant effects.

Type 3 Tests of Fixed Effects					
Plant Type	Effect	Num DF	Den DF	F Value	Pr > F
Forb	Group	1	49.5	14.59	0.0004*
	Census	3	6.38	34.22	0.0003*
	Group*Census	3	139	1.13	0.34
Graminoid	Group	1	49.4	21.60	<.0001*
	Census	3	145	31.17	<.0001*
	Group*Census	3	145	2.15	0.10
Shrub	Group	1	48.8	5.41	0.02*
	Census	3	6.91	3.60	0.07
	Group*Census	3	139	1.33	0.27

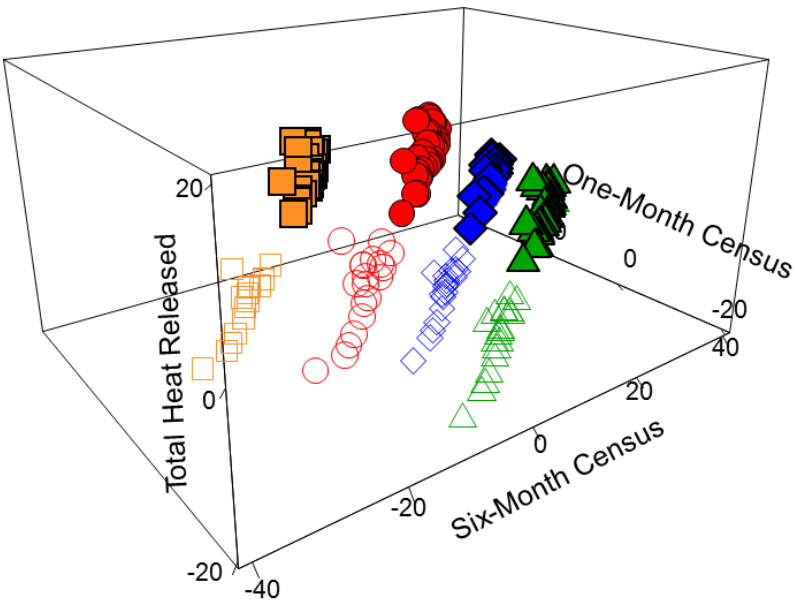

Figure 3.3. Distance-based redundancy analysis ordination (dbRDA) based on distance-based linear model analysis (DistLM) for differences in native species composition between two fire severity groups and four census times. Closed symbols represent low fire severity plots. Open symbols represent high fire severity plots. Green triangles refer to census at one-month. Yellow squares represent the six-month census. Blue diamonds refer to the 12-month census. Red circles represent the 24-month census. Axes 1 and 2 are associated with the six-month census and the one-month census, respectively. Axis 3 is associated with total heat released.

Native species composition was strongly associated with census time and fire severity. Association of census time to species composition emerged from the distance-based redundancy ordination (dbDRA) centered on DistLM analysis. Axis 1 and axis 2 showed clear separation based on time of census when examining overall native species composition (Figure 3.3). Extent of differences in separation was indicated by the distance-based linear model analysis (DistLM). The strongest separation occurred between the one- and six-month censuses, with 12- and 24-month censuses located between the earliest censuses. Axis 1 represented the one-month census and accounted for 41.8% of the fitted variation of the model and 5.8% of the total variation. Axis 2 represented the six-month census and accounted for 26.5% to the fitted variation of the model and 3.7% of the total variation. Axis 3 was associated with total heat released, accounting for 15.6% of the fitted variation and 2.2% of the total variation of the model. The three axes explained 83.8% of the fitted variation and 11.6% of the total variation, hence representing the three most important variables associated with species composition. The accompanying DistLM analysis also indicated a significant association of the one- and six-month censuses and fire severity (Table 3.2). Three census times (one, six, and 24) had a significant association with species composition ($p < .0001$), which may suggest delayed germination from seed bank stock, competition within localized areas, or seasonal changes in species composition. DistLM analysis also indicated a significant influence of total heat released on species composition ($p < .0001$), with a separation visible between both low and high fire severity groups for all census times (Figure 3.3), possibly suggesting an influence of heating.

The association of native species to fire severity appears transient. Examining species composition based on plant type categories showed a clear separation of the fire severity groups at the one-month census (Figure 3.4). The separation between fire severity groups diminished as

Table 3.2. Results of DistLM analysis for differences in native species composition based on all groundcover species between fire severity groups and census times. Total heat released was used to assess accuracy of fire severity group selection. The analysis was based on Bray-Curtis resemblance for square-root transformed data. Each term was tested using 9999 permutations. AIC score for the model was 1649.2. Total heat released and each census time were fixed effects in the analysis. Site was a random effect but did not contribute to the model. *Lygodium japonicum* total frond number/m^2 was used as a covariate in the analysis.

Variables	Sum-of-Squares	F-ratio	P
Six Month Census	25809	8.910	0.0001
Twenty-four Month Census	25839	8.400	0.0001
Total Heat Released	21051	7.048	0.0001
One Month Census	14547	4.967	0.0001
Lygodium japonicum	612907	2.104	0.0001

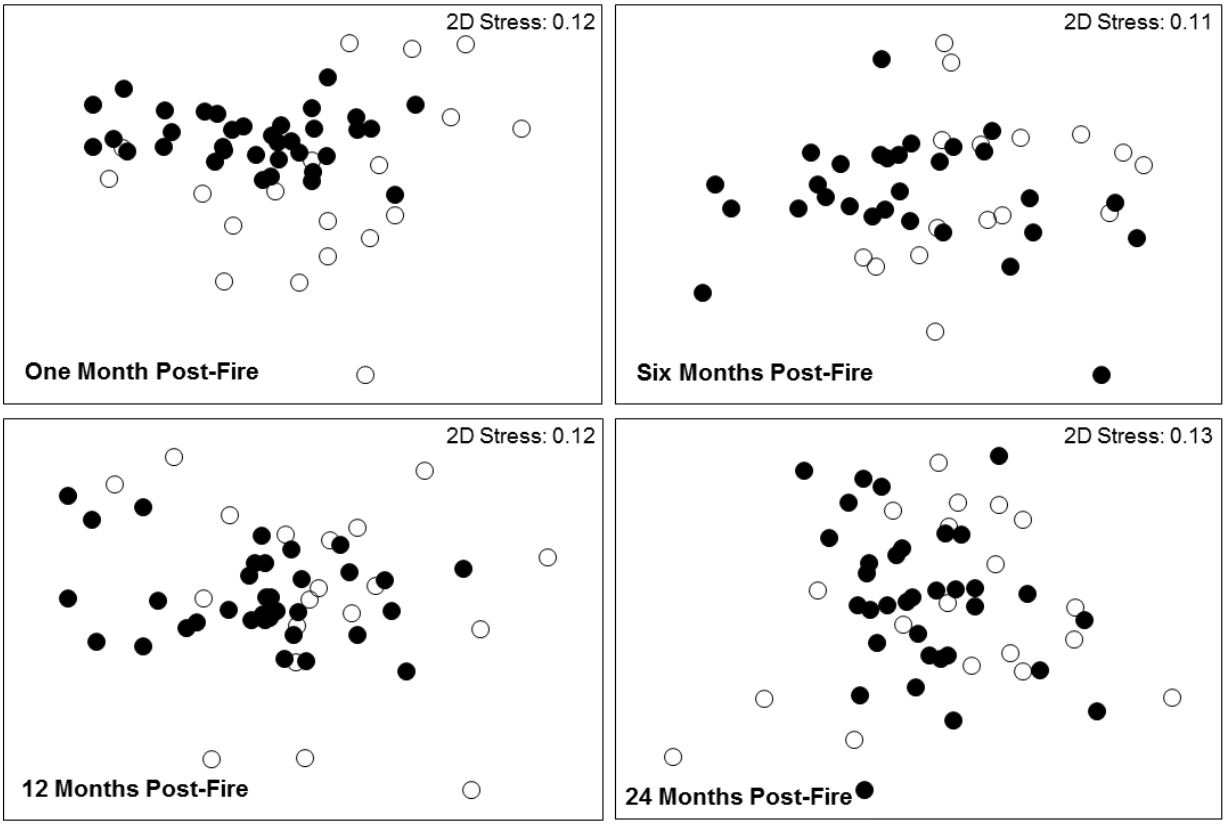

Figure 3.4. Two-dimensional non-metric multidimensional scaling (MDS) ordination illustrating fire severity effects on native species composition at each post-fire census. Plots are arranged by census time (A) one-month (B) six-months (C) 12-months (D) 24-months post-fire. Closed dots represent low fire severity plots. Open dots represent high fire severity plots.

time since fire increased. At the six-month census, species composition among plots for both fire severities began to converge, with less distinct separation. The separation between fire severity groups at the 12- and 24-month census times was not as clear, suggesting fire severity may delay native plant species recovery and have a short-lived influence on native species composition.

Species abundance among plant type categories changed similarly over time. In general, changes in native species abundances were similar among graminoids, forbs, and shrubs during the study (Figure 3.5). The non-metric multidimensional scaling (MDS) plot indicated there was separation in species composition over time (Figure 3.5), as previously observed (Figure 3.3). There was, however, no strong association between any of the three plant types and fire severity groups. This pattern suggests that all plant types were equally influenced by fire severity, with more severe fires depressing abundance.

Changes in native species abundance were observed based on life cycle categories. Annual native species abundances showed the most change associated with fire severity group, with lower abundances occurring in high fire severity locations (Figure 3.6A). Abundance in annual/short-lived perennial species exhibited an initial lag at the one-month census in the high fire severity group, though the difference in abundance dissipated at the six-month census (Figure 3.6 B). Abundance differences after one-month post-fire appear to reflect seasonal changes or response to available resources. Perennial species in the study had a similar change in abundance between fire severity groups at each census (Figure 3.6 C). In each life cycle category, variation in fuel accumulation, which influences heat release, may stunt recovery of native groundcover species in a post-fire environment, and hence have a long-term effect.

Differences in species composition were associated with fire severity. Figure 3.7 is a graphical illustration of specific native species occurring within each fire severity group. Of the

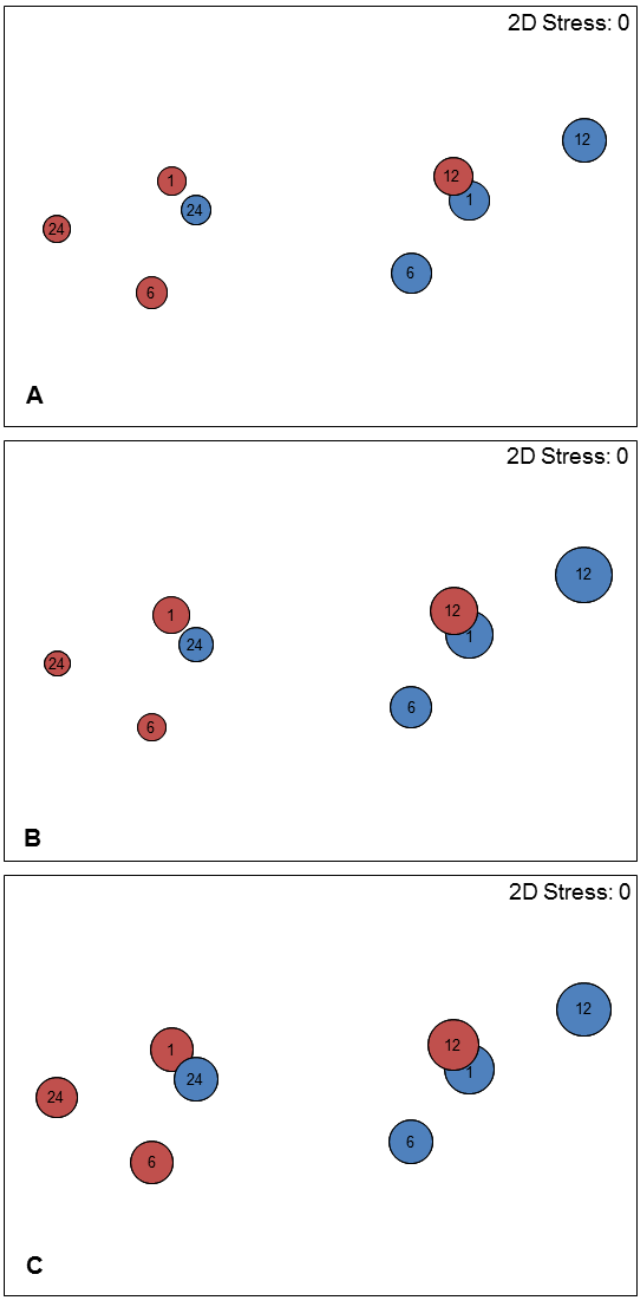

Figure 3.5. Two-dimensional non-metric multidimensional scaling (MDS) ordinations showing native species abundance by plant type category over the 24-month study. All three graphs are the same MDS analysis. Each graph has one of three plant type categories (graminoid (A), forb (B), or woody (C)) overlayed as circles representing abundance. Blue circles represent low fire severity. Red circles represent high fire severity. The abundance of native species is indicated by the size of the circle. Points on each graph represent species abundance data averaged by fire severity group and census time combination. Species abundance represents stem counts/m^2. Size of circles indicate abundance amount. The larger the circle, the more abundant the native species plant type is for that census time. Labels are based on time of census (one, six, 12, 24). Data were square-root transformed with Bray-Curtis similarities.

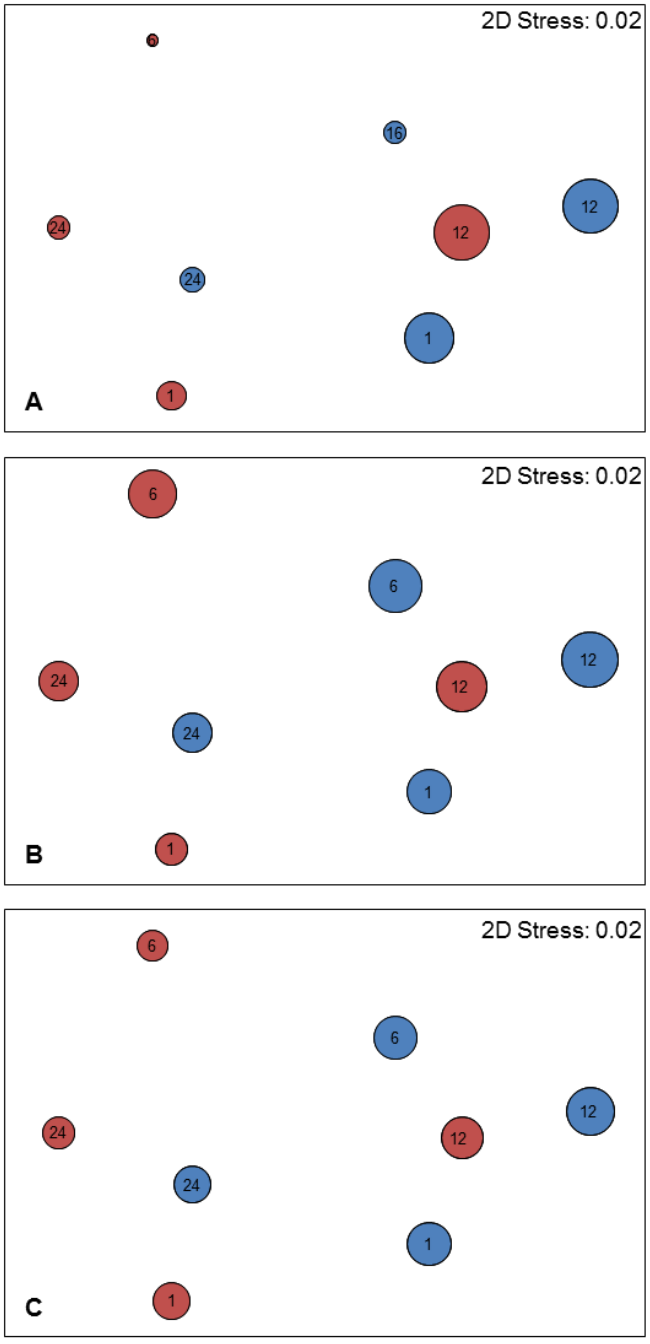

Figure 3.6. Two-dimensional non-metric multidimensional scaling (MDS) ordination showing abundance differences among native species abundance based on life form classification during the 24-month study. All three graphs are the same MDS analysis, but each has one of three life form categories (annual (A), annual/short-lived perennial (B), or perennial (C)) overlayed as circles indicating native species abundance. Blue circles represent low fire severity. Red circles represent high fire severity. Each graph represents species abundance data averaged by fire severity group and census time for each life form category, thus one point per fire severity and census combination. Abundance represents stem counts/m^2. Larger circles indicate greater abundance of native species than smaller circles. Labels are based on time of census (one, six, 12, 24). Data were square-root transformed with Bray-Curtis similarities.

Table 3.3. Output from SIMPER analysis based on native species composition differences between low and high fire severity groups for all census times. Species are listed in decreasing order of contribution to the dissimilarity between fire severity groups, with a cut-off of 70%. Average occurrence for each species in each fire severity group is listed in the first two columns. The Average Dissimilarity is the average of Bray-Curtis dissimilarities for both fire severity groups and is divided into individual species contributions. Diss/SD is the ratio of average contribution of each species divided by the standard deviation of the total contribution for all pairs of samples. The lower the Diss/SD ratio is, the more inconsistent the contribution between one of the fire severity groups (Clarke and Gorley 2006). The last two columns indicate the percentage of contribution from the individual species (Contribution %) and the cumulative total (Cumulative Contribution %). According to Clarke and Gorley (2206), individual species contribution is the most important aspect of the SIMPER output.

Average dissimilarity = 76.39						
	High Fire Severity	Low Fire Severity				
Species	Average Occurrence	Average Occurrence	Average Dissimilarity	Diss/SD	Contribution %	Cumulative Contribution %
Schizachyrium scoparium	0.29	0.7	3.19	1.06	4.17	4.17
Dichanthelium ovale	0.45	0.56	2.79	0.91	3.66	7.83
Rhus copallinum	0.23	0.53	2.76	0.94	3.62	11.45
Dichanthelium sphaerocarpon	0.62	0.57	2.75	0.87	3.6	15.04
Dichanthelium tenue	0.37	0.47	2.65	0.9	3.47	18.52
Stylosanthes biflora	0.33	0.5	2.65	0.92	3.47	21.99
Helianthus angustifolius	0.16	0.41	2.31	0.82	3.03	25.02
Rubus trivialis	0.74	0.75	2.23	0.72	2.91	27.93
Solidago odora	0.23	0.3	1.98	0.75	2.59	30.52
Euphorbia corollata	0.21	0.23	1.76	0.68	2.31	32.83
Schizachyrium tenerum	0.14	0.28	1.76	0.66	2.3	35.13
Symphyotrichum dumosum	0.08	0.32	1.72	0.69	2.25	37.39
Acalypha gracilens	0.25	0.2	1.71	0.69	2.24	39.62
Tephrosia spicata	0.18	0.21	1.54	0.64	2.01	41.63
Tragia smallii	0.16	0.17	1.33	0.57	1.75	43.38
Eupatorium rotundifolium	0.07	0.23	1.29	0.58	1.69	45.07
Smilax glauca	0.16	0.11	1.21	0.52	1.59	46.66
Dichanthelium aciculare angustifolium	0.1	0.17	1.14	0.53	1.5	48.15
Dichanthelium ravenelii	0.11	0.1	1.06	0.45	1.39	49.54
Dichanthelium strigosum	0.03	0.18	1.01	0.45	1.32	50.86
Pinus palustris	0.07	0.11	0.99	0.41	1.29	52.15
Hibiscus aculeatus	0.11	0.08	0.99	0.42	1.29	53.44
Gelsemium sempervirens	0.04	0.16	0.98	0.45	1.28	54.72
Viola primulifolia	0.04	0.17	0.95	0.48	1.24	55.96
Centrosema virginianum	0.14	0.1	0.94	0.49	1.23	57.19
Unknown Sedge	0.05	0.14	0.92	0.44	1.21	58.39
Panicum verrucosum	0.1	0.1	0.9	0.43	1.18	59.57
Eragrostis spectabilis	0.01	0.17	0.89	0.42	1.17	60.74
Vaccinium arboreum	0.03	0.14	0.87	0.4	1.14	61.88
Solidago rugosa	0.05	0.13	0.86	0.42	1.12	63
Desmodium lineatum	0.11	0.09	0.85	0.44	1.11	64.12
Vaccinium darrowii	0.12	0.04	0.84	0.39	1.11	65.22
Gaylussacia dumosa	0.04	0.14	0.84	0.42	1.1	66.32
Phyllanthus caroliniensis	0.07	0.12	0.8	0.43	1.05	67.37
Galactia volubilis	0.1	0.08	0.79	0.42	1.04	68.41
Panicum anceps	0.1	0.06	0.76	0.39	1	69.4

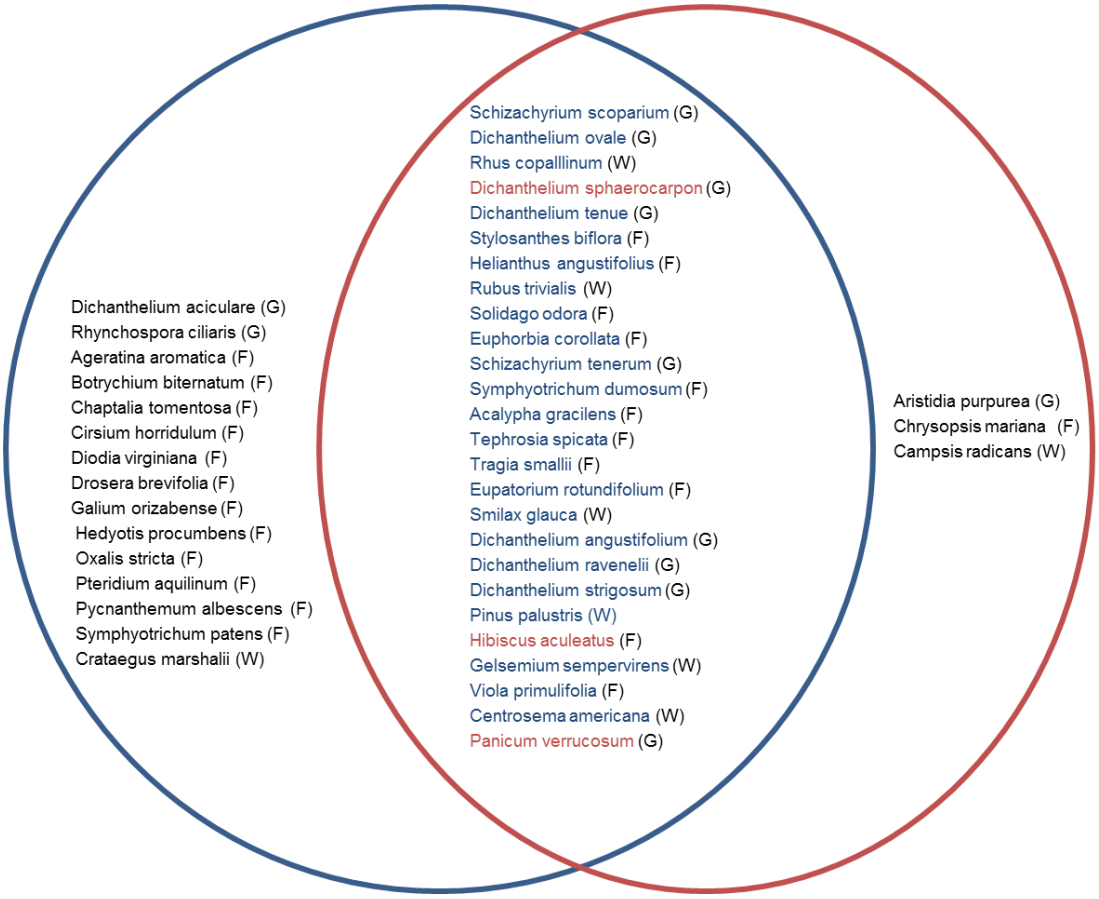

Figure 3.7. Comparison of native species present between fire severity groups over two years following prescribed fires. Species listed within the blue circle represent species only occurring in low fire severity areas. Species in the red circle are those species only occurring in high fire severity areas. Species captured within both low and high severity were selected based on SIMPER analysis. The SIMPER analysis indicated which species were most responsible for differences observed between fire severity groups. Those species contributing to 60% of the difference are listed above in order of their percent contribution (Table 3.3). Species in blue occurred with greater abundance in low fire severity areas. Species in red occurred in greater abundance in high fire severity areas. Plant type classification is indicated for each species (G for graminoid, F for forb, W for woody). Native species data in the SIMPER analysis was presence/absence transformed and *Lygodium japonicum* was used as a covariate.

148 species recorded during the 24-month study, there were 3 species that only occurred in high fire severity areas, whereas 15 different species only occurred in low fire severity areas (Figure 3.7), suggesting differences in species composition. Some species occurring in only one fire severity group, such as *Botrychium biternatum* and *Crataegus marshalii*, were infrequently present in plots, yet others, such as *Campsis radicans* and *Oxalis stricta*, were commonplace among plots during the study. Differences between fire severity groups were supported by ANOSIM analysis ($R = 0.15$; $p < 0.0001$). In Figure 3.7, species listed in the space where the fire severity circles cross represent a subset of species determined by SIMPER analysis as species most responsible for contributing to the overall differences between the two fire severity groups. SIMPER analysis calculated the average contribution of each species to a 70% threshold. Based on this analysis, there was an overall average dissimilarity of 76.4% between fire severity groups. Individual contributions to this difference are listed in Table 3.3.

Fire severity was associated with differences in species abundances among plants occurring in both fire severity groups. *Panicum verrucosum*, an annual grass with prolific seed production (Tucker et al. 2003), contributed 1.18% to the overall dissimilarity (Figure 3.8A). *Panicum verrucosum* first returned at the six-month census with greater abundance in high fire severity locations than in low fire severity locations, which may be related to fall seed production (Plentovich et al. 1999, Leichty 2011). Increased abundance in high fire severity locations persisted though both the 12- and 24-month census times. Abundance of *Dichanthelium ovale*, a short-statured annual/short-lived perennial grass, contributed 3.66% to dissimilarity between fire severity groups. Abundance of *D. ovale* was similar for both high and low fire severity groups, though the greatest abundances were observed at the six- and 12-month census times (Figure 3.8B). The perennial bunchgrass, *Schizachyrium scoparium*, contributed the most to dissimilarity

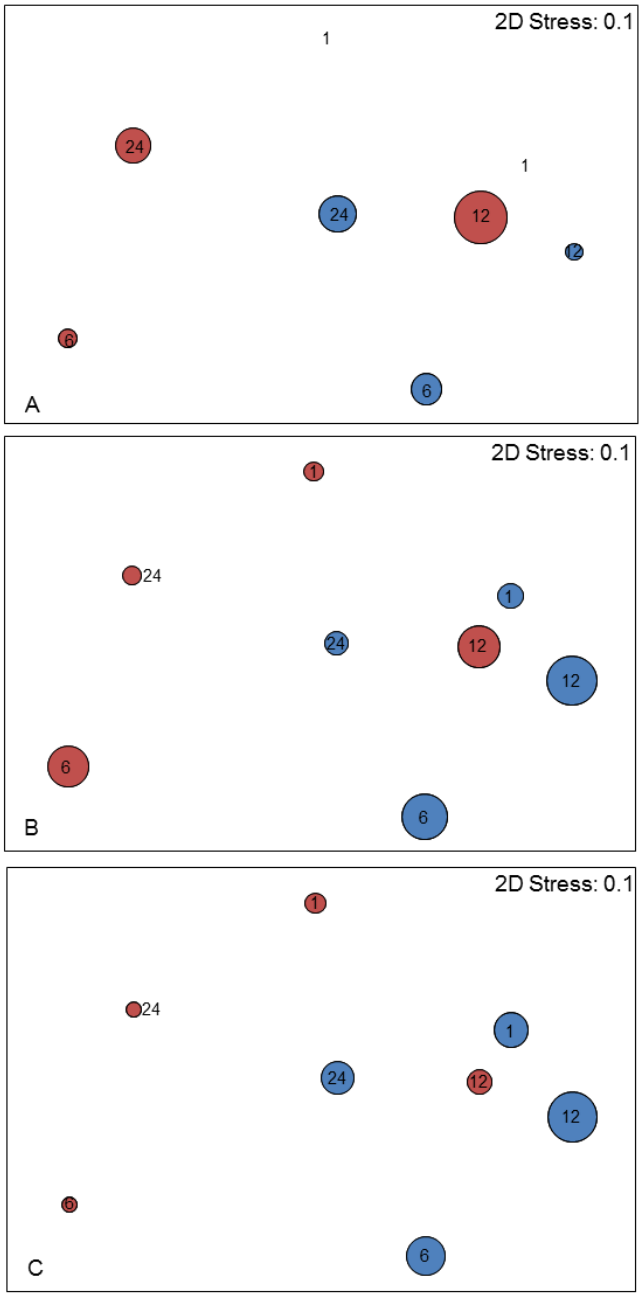

Figure 3.8. Two-dimensional non-metric multidimensional scaling (MDS) ordination illustrating abundance of three native graminoid species. Each graminoid species represents a different life form in the groundcover. (A) *Panicum verrucosum* is an annual. (B) *Dichanthelium ovale* is an annual/short-lived perennial. (C) *Schizachyrium scoparium* is a perennial bunchgrass. Blue circles represent low fire severity. Red circles represent high fire severity. Species abundance data were averaged by each fire severity group and census combination to better visualize changes in abundance over time. Abundance represents stem count/m^2 and changes in abundance are indicated by size of the circle. The larger the circle, the more abundant the graminoid is at that census time. Plots are labeled by census time (one, six, 12, 24). *Panicum verrucosum* was not present at the one-month census for either fire severity group. Data were square-root transformed with Bray-Curtis similarities.

between fire severity groups (4.17%) and was observed to have greater abundance in low fire severity plots for all census times (Figure 3.8C). The association with low fire severity areas may be correlated to heat release through fuel accumulation.

Discussion

Fuel accumulation has been commonly used to predict severity of fire in the pine savanna. Fire severity, the extent to which aboveground biomass is combusted during fires, (Neary et al. 1999, Bond and Keeley 2005, Keeley et al. 2008, Keeley 2009), is widely recognized to be dependent on pre-fire fuel loads (Keeley et al. 2008, Pyke et al. 2010). The amounts of fuels in the groundcover of pine savannas tend to be determined by abundances of dominant species (Harrington 2006), which include bunchgrasses along with resinous pine needles shed from overstory pines (Grace and Platt 1995, Thaxton and Platt 2006). These two components produce flammable fuels that facilitate fire spread in the understory (Brockway et al. 2006, Gagnon et al. 2010). The amounts of such fuels within localized areas thus should contribute to the total heat released (Johnson and Miyanishi 1995). Locally variable accumulation of these fine flammable fuels might be expected to generate a range of fire severities within pine savanna groundcover, even in a single fire (Hiers et al. 2009).

Results of the study were partially consistent with this hypothesis. Total heat released during a prescribed fire in a restored pine savanna tended to increase with biomass of groundcover fuels. Low fuel accumulation in the groundcover was strongly associated with low fire severity and reduced heating because there was little biomass present to burn (also see Donato et al. 2009). The study suggested, however, that caution is needed when using fuel accumulation to predict severity of fire in frequently burned pine savannas. Large pre-fire fuel loads did not always yield greater total heat released. While high fuel loads seem to be necessary,

other factors may influence whether high fire severity will result during a fire. Types of fuels present have been shown to decrease consumption through fuel chemistry, moisture content, and particle size regardless of quantity present (Keeley et al. 2008, Pyke et al. 2010, Bernhardt et al. 2011). Areas with mostly fine-fuels, such as graminoids and forbs, are more likely to support fire ignition and spread then areas dominated by woody species (Mitchell et al. 2006). Empirical post-fire measurements thus appear to be needed to specify high fire severity, especially if valid inferences are to be made about ecological effects of fire severity (Gutsell and Johnson 2007), such as on species composition of the diverse groundcover of pine savannas.

Fire severity produces transient changes in species richness over the two-year post-fire period. Disparities in total heat released in the study generated two distinct fire severity groups, and these differences were strongly associated with initial species abundance differences one-month post-fire in native groundcover species. Reduced abundance in locations with greater fine-fuel accumulation may have occurred because heated soil may damage or kill both seeds and perennating buds (Pyke et al. 2010). Localized areas experiencing longer heating duration, and as a result greater total heat released at ground level, may incur damage to reproductive structures and subsequently reduced re-sprouting or germination (Gagnon et al. 2010). Reduction in abundance was clearly observed in both graminoid and forb species during the experiment and supports previous studies highlighting how fire severity, through fuel load, may negatively influence regrowth in a post-fire environment (Grace and Platt 1995, Mitchell et al. 2006, Zimmermann et al. 2008, Myers and Harms 2009a). While reduced abundance in high fire severity groups was recorded at the one-month post-fire census, abundances of native species at progressive census times began to converge. Dissimilarity in species composition and abundance, however, may be maintained until the next fire disturbance. Differences in post-fire

species abundance appear to initially be affected by variation in fire severity and may be further influenced by local variation in recruitment from seed banks or seed rain from the nearby species pool (Keddy et al. 2006, Myers and Harms 2009b), on-site competition and predation (Zimmermann et al. 2008) or variability in resources, such as light and space availability (Bond and Keeley 2005, Platt et al. 2006). One implication of the study is that high fire severity areas may transiently expose groundcover to invasion shortly after a fire. As time since fire increases, ability for successful invasion by exotic species declines. Successive fires with variable severity may result in more opportunity for successful invasion, thus influencing local groundcover plant species diversity.

Groundcover species composition was associated with fire severity across all plant types. Fire severity is tied both to soil heating and biological responses of species within burned areas. Resiliency of species to heating may influence species composition in the post-fire environment (Keeley et al. 2008, Pyke et al. 2010), with some plants being more capable of withstanding high fire severities (White et al. 1996, Bernhardt et al. 2011). For example, native groundcover species of frequently burned habitats, such as pine savannas, are more often highly resilient to high fire severities (e.g., Gagnon et al. 2010). In this study, changes in abundance with fire severity occurred for graminoids, forbs, and woody species; the rank order of contributions to dissimilarity between fire severity groups were similar to their rank order of abundance. Graminoids and forbs tended to be the most common plant types, and these species contributed more to effects of fire severity on species composition and abundance in groundcover than woody species, a pattern also observed in other studies (Mitchell et al. 2006, Platt et al. 2006 and references within). The suggestion from the data is that graminoids and forbs may be more differentially affected by high severity fires than woody shrubs and vines, perhaps because roots

or rhizomes of woody plants tend to be more protected or located deeper in the soil (cf. Gagnon et al. 2010). Although graminoids and forbs may be affected more by high severity fires, all plant types were suppressed under high fire severity conditions in the pine savanna.

Sensitivity to fire severity also differed among different plant life cycle categories. Annual species contributed much less to differences in species abundance in low and high fire severity plots than either annual/short-lived perennials or perennials. Difference in contribution could be tied to how annual species respond to fire severity in the post-fire environment. Annual species in the pine savanna may be more sensitive to heating of soil, especially if plant species persist via dormant seeds than those that persist via perennating structures. Initial low abundance of annuals in all plots may have resulted from prescribed fire occurring during the late spring/early summer transition. These prescribed fires are designed to mimic lightning-ignited fires typical of pine savannas (Platt 1999, Frost 2006), therefore native annual species that have evolved within this system may have mechanisms appropriate for survival, including reproductive responses triggered in the post-fire environment (Brooks et al. 2004, Brewer et al. 2009). Prominent annual species (e.g., *Panicum verrucosum*), germinate from the seed bank in both fire severity groups. The difference, however, between fire severity groups may be tied to seed bank heating, in which high fire severity locations reached heating duration outside of a survivable range.

Similar differences in abundances between fire severity groups were also observed for annual/short-lived perennial and perennial species. Heating duration may be an initial negative effect for species in all three life cycle categories, lessening nutrient reserves via aboveground biomass replacement. The negative effects, however, may be a short term response to open canopy, during which increased light availability may result in a surge of abundance as time

since fire increases. For example, removal of aboveground biomass and greater light availability at ground level may stimulate the increased abundance of short-statured *Dichanthelium ovale* in open areas.

Variability of fire severity leads to heterogeneity in the availability of important resources. Light availability has been documented as a key abiotic component of groundcover species diversity in the pine savanna influenced by fire (Brewer and Platt 1994, Brewer 1999b, Bond and Keeley 2005, Platt et al. 2006, Thaxton and Platt 2006, Walker and Silletti 2006, Brewer et al. 2009). Low-intensity fires consume fine-fuels and aboveground biomass, opening space and increasing light penetration in the understory, thus providing opportunity for colonization, establishment or re-emergence by groundcover species. Within newly opened areas, there is equal opportunity for establishment and regeneration by native groundcover species. Competition may increase with increasing time since fire because light intensity reaching the ground level diminishes, leading to a shift in representation of species comprising the groundcover. Increased light levels may explain increased abundance for one or both fire severity groups in all three life cycle categories. Heterogeneity of fire severity also contributed to the degree of abundance change and was specific to individual species, even species occurring within the same genus, such as differences observed within the genus *Dichanthelium*. Sensitivity to high fire severity was observed in *D. ovale* and *D. strigosum* (Figure 3.7), yet *D. sphaerocarpon* seemed to benefit from higher fire severity areas (Figure 3.8). Variation in abundance within the genus suggests fire severity plays a role in elimination of competition among congeners within the seed bank, as well as functional groups, allowing small-statured species opportunity to establish and replenish the seed bank. High fire severity also was beneficial to *Vaccinium darrowii*, a perennial woody species which displayed a similar increased

abundance in high fire severity areas. Menges and Kohfeldt (1995) observed similar results, suggesting *V. darrowii* benefits from increased light availability in the post-fire environment. Areas that experienced more severe fires may have reduced competition via damage to belowground perennating structures, thus allowing increased abundance of species tolerant to prolonged heating duration.

Variation in fire severity may provide opportunity for invasion by native and exotic species. Based on the results of the study, species composition varied at each census time and an association with the degree of variation in fire severity was apparent. The variation of fire severity may promote plants with particular traits that aid in colonization and establishment within the post-fire environment (Bond and Keeley 2005). For both native and exotic species, plants with short life cycles, high seed production and the capability to attain a height that captures valuable light resources may be more successful (Grime 1977, Masocha et al. 2011). In areas of high fire severity, plants with belowground perennating structures may also survive recurrent fire. Thus rapidly colonizing species that establish belowground structures may be prominent in frequently burned pine savannas. Through frequent fire return and variation in fire severity, opportunities occur for species possessing these traits. For example, Japanese climbing fern (*Lygodium japonicum*) has invaded the longleaf pine savanna despite restoration efforts (Chapter 2, Leichty et al. 2011b). Japanese climbing fern is capable of abundant spore production, and once established, generates extensive belowground rhizomes along with long, twining aboveground fronds (Minogue et al. 2010). Experimental examination indicates that *L. japonicum* genets are surviving and increasing with current restoration efforts (Chapter 2). While biennial prescribed fires are benefiting native groundcover species, these fires also allow existing fern genets to recover and open space for spores to establish and develop young sporophytes. As

sporophytes mature, subterranean rhizomes form and allow for survival of the genet through subsequent fires.

Fire may expose the longleaf pine savanna to invasion during restoration. The conundrum resulting from necessary restoration efforts to manage native species that also generate opportunities for invasion is not unique to the pine savanna (D'Antonio and Vitousek 1992, D'Antonio and Meyerson 2002, Keeley et al. 2008). Studies have documented how fire is associated with non-native plant invasion (Kuenzi et al. 2008 and references within, Pyke et al. 2010, Masocha et al. 2011). Fire is an important component for the maintenance of native plant diversity in the longleaf pine savanna (Platt 1999, Walker and Silletti 2006). Although I did not have pre-fire data on native species composition, Camp Whispering Pines has been managed with biennial fires for over 20 years, and species diversity has been well-documented (Drewa et al. 2006, Platt et al. 2006, Myers and Harms 2009a). Without frequent fires, increased encroachment of woody species and decline of herbaceous plants would occur (Platt 1999, Passmore 2005, Frost 2006, Peet 2006, Thaxton and Platt 2006). The frequent biennial fires at Camp Whispering Pines, however, generate openings in the understory through consumption of flammable fuels at various fire severities, thus providing "windows of opportunity" for invasion. Consideration of fire return, coupled with severity of fire, compound the effectiveness of fire as a restoration tool, with hotter fires potentially creating more opportunities for invasion. The potential for invasion by exotic species necessitates clearly defined restoration goals and increased understanding of the ecological role a particular invasive species may play within the introduced environment.

Fire can be responsible for cascading changes in species composition and abundance. Fire frequency and light availability are often cited for maintaining and/or influencing

biodiversity in savannas ecosystems (Bond and Keeley 2005, Harrington 2006, Keddy et al. 2006, Mitchell et al. 2006, Platt et al. 2006, Walker and Silletti 2006, Myers and Harms 2009a). Fire severity appears to play an important role, but a single event may not adequately predict regeneration of post-fire vegetation (Keeley et al. 2005, White et al. 2006, Keeley et al. 2008). Rather, multiple fires, with varying fire severities, at the same location must be considered when evaluating fire severity influence on species composition. Microsites that experience variation in fire severity could, therefore, be on separate, but intersecting trajectories in which differences in species composition fluctuate among microsites depending on previous fire severity. According to Keeley et al. (2008), "fire history is an important determinate of fire severity." Areas where greater fuel consumption and subsequent heat release occur may exhibit a lag in native species composition in comparison to nearby locations of low fire severity. While there were a select few species tolerant of increased heating and fire severity, the majority of species comprising native groundcover diversity were lower in abundance in high fire severity areas, producing delayed recovery and re-establishment. Future work should include long-term examination of microsite species composition with varying fire severities. I postulate that species occurring in both low and high fire severities should differ in abundances based on previous occurring fire severities within that location.

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Chapter 4

The Effect of Tree Falls on Japanese Climbing Fern Abundance in a Restored Longleaf Pine Savanna

Introduction

The structure of many ecosystems is maintained by disturbances. Recurrent, abiotic (e.g., hurricanes, fires) and biotic (e.g., animal-generated biopedturbation) disturbances influence both physical and biological components of ecosystems (Clements 1916, Mushinsky and Gibson 1974, Platt 1975, Pickett 1976, White and Jentsch 2001, Passmore 2005, Eldridge et al. 2009). Such disturbances can be categorized based on the spatial scale at which they occur. For example, in pine savannas, large-scale disturbances, such as windstorms (Platt 1999, Beckage et al. 2006) tend to affect landscapes (e.g., Hoctor et al. 2006), whereas small-scale disturbances, such as ant mounds or burrowing activity by animals (Hermann 1993, Means 2006) may influence only a few meters of a localized area. Both scales of disturbance may be important for maintaining groundcover biodiversity. Frequent low-intensity fires sustain the diverse groundcover vegetation of longleaf pine savannas by altering the physical environment, creating gaps in the understory, and releasing resources (Platt 1999). Further, biopedturbations (sensu Whitford and Kay 1999, Eldridge et al. 2009) resulting from burrowing of animals such as the gopher tortoise, both reduce shrub establishment and promote increased growth and spread of herbaceous species in pine savannas (Diemer 1986, Hermann 1993, Simkin and Michener 2005). Interactions among such disturbances, and the frequency with which they occur, can influence species composition within an ecosystem.

Longleaf pine savannas are shaped by fire and wind disturbances. Fire is the most frequent large-scale disturbance of the pine savanna, with lightning-ignited fires occurring at least 2-3 times a decade during the dry spring-wet summer transition (Platt et al. 1988b, Platt 1999, Varner et al. 2005, Beckage et al. 2006, Frost 2006, Peet 2006). Occurring within a short return interval, fire consumes flammable fine-fuels and reduces woody shrubs, while

simultaneously promoting high biodiversity groundcover by releasing seeds from dormancy and creating gaps in the understory (Olson and Platt 1995, Drewa et al. 2002, Platt et al. 2006, Myers and Harms 2009a, Glitzenstein et al. 2012). Fires in pine savannas are dependent on the arrangement and accumulation of flammable fuels, which can result in spatially heterogeneous consumption of fuels in the understory. The arrangement and accumulation of flammable fuels are dependent on windstorms. Windstorms, such as hurricanes, are periodic disturbances that occur 1-2 times a decade (Batista and Platt 1997) toward the end of the wet summer season. Such disturbances affect forest structure and composition in pine savannas (Platt and Rathbun 1993, Turner et al. 1997, Beckage et al. 2006) by changing canopy structure, fuel distribution (Platt et al. 2000, Gilliam et al. 2006), and stand density (Turner et al. 1997, Palmer et al. 2000). Openings in canopy cover lead to heterogeneous light levels and patchiness of fuels in the understory (Platt and Rathbun 1993, Platt et al. 2006). The canopy damage may range from severe (e.g., uprooting of trees, snap-offs) to minor (e.g., pine needle removal). As intensity of windstorm increases, downed tree crowns and boles would be anticipated, thus generating greater accumulation of fine-fuels in a localized area. Local variation in fires can influence changes in groundcover composition, creating a patchy mosaic of herbaceous groundcover in longleaf pine savannas (Glitzenstein et al. 1995, Brewer et al. 1996).

Stumps (tree bases) may result from the occurrence of lightning strikes or windstorms. Lightning strikes are a common occurrence in the Gulf Coastal Plain (Van Lear et al. 2005), with an average flash density between 6-9 flashes/km^2/year (Orville et al. 2011). The frequency with which lightning strikes occur ensure that some individual trees are hit, albeit at a low rate. When lightning does strike a tree, a stump may be produced. A stump is formed when the crown and majority of the bole are severed from the tree base. Removal of the crown creates an opening in

the canopy, altering light reaching understory vegetation. During an intense windstorm (e.g., hurricane), multiple trees may be tipped over, with roots exposed, or snapped off with jagged breaks in the bole (Platt et al. 2002). Intense windstorms also occur at a low frequency, but their extent is large and several stumps can be produced. Both lightning strikes and windstorms ensure stumps are continually present in the pine savanna.

The presence of stumps may result in increased animal activity. A stump is an important microsite for burrowing and non-burrowing animals, providing locations to escape extreme temperatures, areas to forage, and refuge from predators (Hermann 1993, Means 2006). Both the stump and associated roots contain oleoresin-impregnated heartwood that may resist decay for years, yet is surrounded by an outer layer of sapwood, which decays quickly and is a soft substrate for digging (Means 2006). The initial decomposition of sapwood by microorganisms and decomposers may attract additional foraging organisms to this recent food source (Means 2006). Successive foraging organisms may arrive at stump locations and manipulate the surrounding soil substrate to extract resident prey organisms as sapwood continues to decompose (Hermann 1993, Simkin and Michener 2005). As sapwood decays, more heartwood is exposed. The heartwood insures longevity of the stump and prevents root cavities from collapsing (Means 2006, Mitchell et al. 2009). Recurrent fires may cause the resin in heartwood to burn, but it typically requires multiple fires for complete combustion of the stump (Means 2006). Stumps subjected to repeated fires should have less heartwood and greater decomposition of sapwood than stumps that have experienced only a few fires. This differential decomposition may result in a prolonged, but nonpermanent localized site for animal biopedturbation because of the openings and changing soil conditions surrounding the stump.

The persistence of a stump and the associated animal biopedturbations may influence groundcover species. The activity of soil disturbance agents modifies plant species composition and soil structure in a number of different ecosystems (Platt 1975, Simkin et al. 2001, Eldridge et al. 2009). Soil burrowing organisms, such as ants (Lubertazzi and Tschinkel 2003), crawfish (Brewer 1999a, b), and gopher tortoises (Hermann 1993, Aresco and Guyer 1999) have been hypothesized to engineer longleaf pine savannas through extensive, but small-scale soil manipulation. The influence of animal disturbance on species composition may have both positive (Platt 1975, Simkin et al. 2001) and negative effects (Rapp and Rabinowitz 1985) on the colonization and establishment of individual plants. For instance, many animals disrupt localized areas, burying plants in mounds of soil when constructing burrows or through foraging activities (Hermann 1993, Simkin et al. 2001, Simkin and Michener 2005, Means 2006).

The effects of animal biopedturbations may depend on the local environment. Increased light availability at ground level would be expected in areas with stumps because overstory trees have been removed by windstorms, lightning strikes, insect infestation, etc. Some plant species may benefit from increased light availability and exposed soil patches for colonization that result from biopedturbations surrounding stumps. Removal of an overstory tree, coupled with increased small-scale animal disruption thus may lead to changes in localized groundcover composition.

The combination of abiotic and biotic disturbances may influence invasion by non-native species in longleaf pine savannas. Disturbances have been recognized as facilitating invasions by non-native species (Hobbs and Mooney 1991, D'Antonio and Vitousek 1992, Hobbs and Huenneke 1992, Kwit et al. 2000, D'Antonio and Meyerson 2002, Setterfield et al. 2005, Martinson et al. 2008). One hypothesis is that resources are made available (resource opportunity; Shea and Chesson 2002, Shea et al. 2004). The disturbances occurring in the

longleaf pine savanna open canopy gaps, increase light levels at the ground surface, while animals manipulate the soil, potentially releasing resources. One species that may benefit from the pooled effect of disturbances is Japanese climbing fern (*Lygodium japonicum*).

Japanese climbing fern may benefit from localized abiotic and biotic disturbances in longleaf pine savannas. Japanese climbing fern, an Old World species native to temperate, subtropical and tropical regions of eastern and southeastern Asia and northern Australia (Singh and Panigrahi 1984, Munger 2005, Van Loan 2006b, Willis et al. 2006, Mehltreter et al. 2010), is invading southeastern Gulf Coast longleaf pine savannas (Leichty et al. 2011a). This perennial fern indeterminately spreads by long, twining fronds aboveground (Clarke 1936, Mueller 1982, 1983, Van Loan 2006b), which are capable of abundant spore production that germinate and mature in moist, open environments (Murtaza et al. 2004, Munger 2005, Engelman and Nyland 2006, Mehltreter et al. 2010). Subterranean rhizomes allow for vegetative expansion and persist approximately 1-3 cm below the soil surface (Chapter 2, Munger 2005). The generation of a stump may expose localized areas in the groundcover to increased colonization by *L. japonicum*, especially after a windstorm coupled with rain (e.g., thunderstorm, hurricane). Additionally, animal disturbance activities surrounding the stump may expose soil patches that could then be colonized by *L. japonicum* spores. The increased light levels from canopy gaps, along with greater moisture availability and exposed soil, may yield adequate time for subterranean rhizome establishment and ensure persistence of the fern though frequent fires in the longleaf pine savanna. These areas of soil disruption, therefore, may act as windows for establishment of this invasive fern.

In this study, I examine effects of tree stumps and animal disturbances on Japanese climbing fern in the groundcover of a restored longleaf pine savanna. Specifically, I addressed

whether tree stumps influence animal-generated disturbances and Japanese climbing fern occurrence. I studied the occurrence of biopedturbations and *L. japonicum* in localized areas containing stumps and nearby similar-sized areas without stumps. Secondly, I determined if abundance of animal-generated disturbances and densities of fronds in *L. japonicum* genets varied among stumps in different stages of decomposition. I expected to find a fluctuation of animal activity surrounding stumps that is dependent on the degree of decomposition and fire consumption over time. I hypothesized that stumps will have increased animal activities, which in turn will result in increased frond densities of Japanese climbing fern, compared to areas without stumps. Further, I predict frond genets to be greater in areas of open canopy, where more light is available, than in areas of closed canopy.

Methods

Study Site: Girl Scout Camp Whispering Pines, the site of the field study, is located in Tangipahoa Parish in eastern Louisiana. Camp Whispering Pines is an upland mesic site situated on loess-capped fine sand soils (McDaniel 1990, Roth et al. 2008) that contains a relatively intact overstory comprised of longleaf pine (*Pinus palustris*) and a diverse herbaceous understory, which includes bluestem grasses, such as *Schizachyrium scoparium* and *S. tenerum* (Platt et al. 2006, Myers and Harms 2009a). The site has experienced different land uses over the past century, including fire suppression, habitat fragmentation, open range cattle grazing, and logging (Platt et al. 2006, Leichty et al. 2011a). Increased abundance of woody shrubs and reduced herbaceous groundcover has been a consequence of decades of fire suppression (Passmore 2005, Thaxton and Platt 2006). The abundance of shrubs has declined and herbaceous groundcover has increased in upland pine savanna over 20 years of restoration involving growing-season

prescribed fire (Platt et al. 2006, Thaxton and Platt 2006, Myers and Harms 2009a, Leichty et al. 2011a).

Ecological restoration has been ongoing at Camp Whispering Pines since 1990. A general description of the goals and methodology is provided by Platt et al. (2006). In 1996, several areas separated by roads and tent units within the camp were selectively logged for ecological management, leaving pine stumps. These pine stumps were burned to various degrees during subsequent prescribed fires; after each fire, some stumps remained intact, but others were partially to completely consumed, leaving tree bases and holes of varying sizes. Removal of trees altered canopy cover within localized areas and increased light availability reaching the understory herbaceous groundcover. Evidence of animal activity has been observed surrounding stump areas. Based on these restoration activities, Camp Whispering Pines provides an opportunity to investigate disturbance effects in a longleaf pine savanna.

Restoration at Camp Whispering Pines has relied on prescribed fires to restore the longleaf pine ecosystem. The prescribed fires have been conducted biennially since 1992 during the late spring-early summer transition (April-May) (Platt et al. 2006, Leichty et al. 2011a). Prescribed fires during this three-year study occurred in 2008, approximately 10 days after rain. Two blocks were selected within the area to be burned. The two blocks were burned at different times on the same day. On the day of the fire, maximum air temperature was between 26.7-28.8 ^{o}C, average humidity was 100%, and wind speeds were 4.8 km/hr with maximum wind gusts reaching approximately 38.6 km/hr. Each block was ignited separately, though all plots within a block burned as part of the larger fire. All fires burned across the sites as flanking-head fires (in front of winds of 2.24-6.71 m/s) with flame lengths typically 0.5-2 m.

Disturbance Study: I studied how the presence of a stump influences native and invasive species occurrence and density (numbers/m^2) of animal-generated disturbances by examining locations within the pine savanna in the vicinity of tree stumps. I established 94 paired plots within approximately 200 hectares of upland longleaf pine savanna comprising two different fire blocks at Camp Whispering Pines in spring 2007 before prescribed fire. Paired plots were selected as randomly as possible. One member of each pair of plots was located around a stump; stumps were in different stages of soil disruption. Stumps were placed into one of three categories based on arrangement of surrounding soil and degree of soil disruption. First, an "intact stump" lacked soil disruption, with surrounding soil tightly compressed against the base. Second, "partial stumps" exhibited some decomposition, often were partially burned, and had loss of soil around the base. Third, a "stumphole" occurred where the majority or the entire stump was no longer present. A completely formed hole consisted of a soil depression at least 10 cm deep and exhibited obvious indication a stump had been present (e.g., wood fragments, lateral root cavities). Figure 4.1 illustrates the differences in average stump size based on these three categories. Size of the circular plots (diameter of 1.20 m; area of 1.13 m^2) was determined after conducting a preliminary examination of average pine stump diameters. The second member of each pair was a control plot without a stump or stumphole; this plot was randomly established about 5 m from the stump plot subject to the constraint of no stumps or other recent disturbances present. The size of sampled area within the control plots was adjusted for the size of the stump in the paired plot to keep sampling area the same.

All paired plots were placed so that overstory pine canopy was or was not present to compare single tree snaps to areas of multiple downed trees. Open canopy areas were designated as those where paired plots were >10 m from surrounding trees (sensu Platt et al. 2006).

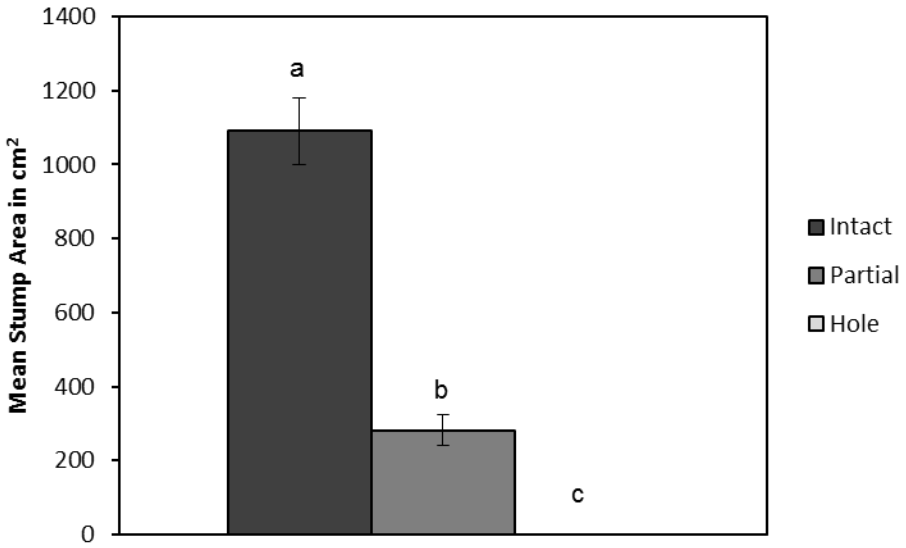

Figure 4.1. Mean area of intact stumps, partial stumps, and stumpholes of longleaf pine at Camp Whispering Pines. Vertical bars represent mean ± one standard error. Means with the same letter are not significantly different (LS Means comparison).

Closed canopy areas were classified as locations where the overstory was continuous and bases of surrounding trees were < 10 m away from plots. As a result, live trees were closer to the stump and paired control plot in closed canopy than in open canopy areas. During the study, Hurricane Gustav (2008) generated additional stumps and influenced canopy cover in some locations.

Plots were annually censused one-month post-fire from 2007 through 2009. At each census, stump area was measured approximately 15 cm from the soil surface to track changes in stump size. Disturbances generated by animals were distinguished from physical sloughing of soil by the presence of scat, prints, or other evidence of animal activity. These biopedturbations were categorized as a burrow (e.g., crawfish turret, rodent burrow) mound (e.g., fire ant mound), or dig (e.g., foraging activity that did not result in tunnel construction). Each disturbance was marked with a unique tag capable of surviving fire.

Stem counts were recorded for all groundcover species rooted within each plot. Plants were identified to species and placed into the following category: graminoid, forb, or woody. Graminoids contained species in *Cyperaceae* and *Poaceae*; forbs consisted of other herbaceous species and ferns; and woody species included hardwood shrubs and vines. Native and invasive species were distinguished within each plot as well. Four invasive species were recorded at Camp Whispering Pines during the field study: *Ligustrum sinense* and *Triadica sebifera* (woody species), *Lonicera japonica* (vine), and *Lygodium japonicum* (fern). All fronds rooted within a plot were considered part of one genet of *L. japonicum*. A complete census of all plots did not occur in some years. Time constraints reduced sampling in some years and plot destruction occurred during salvaging operations after Hurricane Gustav.

Statistical Analysis: The statistical analyses were conducted using procedures in SAS 9.1.3 (SAS 2003). The procedure Proc Means was used to obtain basic statistics, included means and standard errors for density of native and invasive species and animal disturbances. Mixed model analyses were conducted using Proc Mixed with $\alpha=0.05$ with LS Means comparisons. For the mixed analyses, compound symmetry covariance structure (CS) was used in the Repeated statement to account for equal time steps between censuses. The Proc Mixed procedure was also used to test for differences among disturbance treatments, canopy cover, and census times during the duration of the study for animal-generated disturbances and *L. japonicum* occurrence and genet size. Orthogonal contrast comparisons were determined *a priori* to assess the effects of disturbance treatment, canopy cover, and fire occurrence on animal-generated disturbances abundance in a mixed model analysis. Data were log transformed to achieve normality.

Results

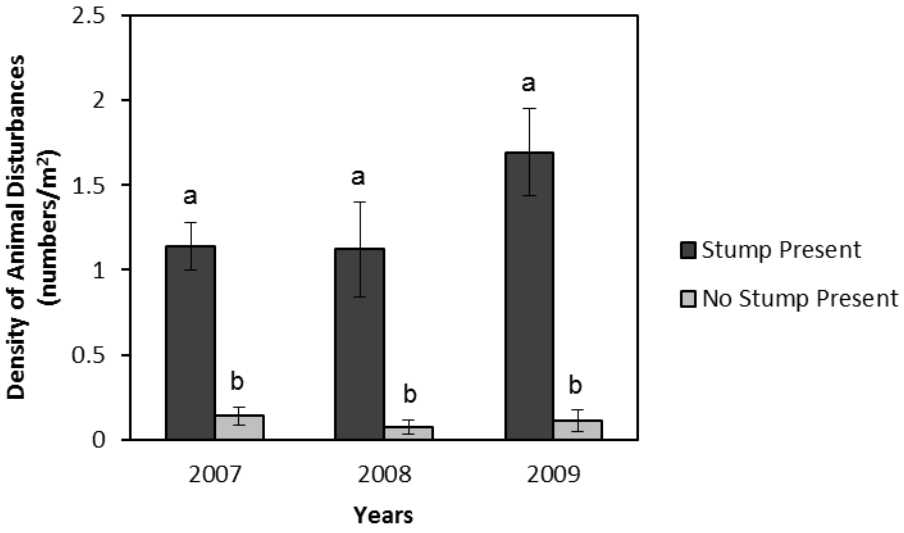

Figure 4.2. Mean density of animal-generated disturbances (number/m^2) around stumps and in similar-sized paired areas without stumps. Data for stumps were averaged over state of decomposition. Vertical bars represent mean $\pm$ one standard error. Means with the same letter are not significantly different (LS Means comparison).

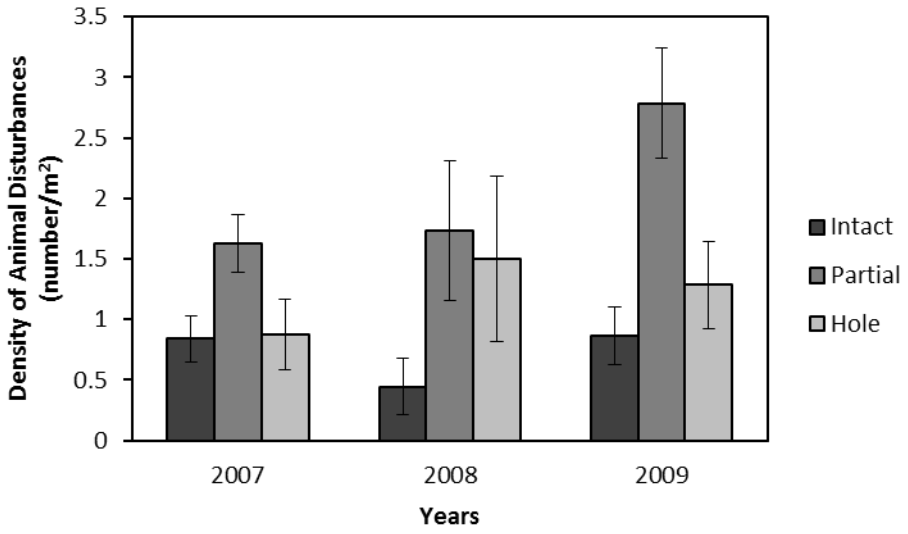

Figure 4.3. Mean density of animal-generated disturbances (number/m^2) around intact stumps, partial stumps and stumpholes in similar-sized areas without stumps. Vertical bars represent mean $\pm$ one standard error.

Table 4.1. ANOVA table displaying effects of stump types, year of sampling, canopy cover, and their interactions on abundance of animal-generated disturbances in pine savanna. Data were log transformed and analyzed with Proc Mixed procedure in SAS 9.1.3. Stump type denotes one of six stump treatments and the corresponding areas without a stump (intact, intact control, partial, partial control, stumphole, stumphole control). Year refers to the year sampling of plots occurred (2007, 2008, 2009). Canopy cover refers to open or closed canopy cover. The AICC was 289.6. An asterisk (*) indicates a significant effect.

Type 3 Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Stump Type	5	49.7	24.17	<.0001*
Year	2	6.32	1.49	0.30
Stump Type*Year	10	49.2	0.89	0.55
Canopy Cover	1	106	0.00	0.98
Stump Type*Canopy Cover	5	115	0.38	0.86
Year*Canopy Cover	2	108	0.40	0.67

Table 4.2. Orthogonal contrasts comparing disturbance treatment (stump present or absent) and stump type (intact stump, partial stump, stumphole) effects on animal-generated disturbance abundance in the longleaf pine savanna. Orthogonal contrasts were established *a priori*. All statistical comparisons were conducted using SAS 9.1.3 with α=0.05. As asterisk (*) indicates a significant effect.

Contrasts				
Comparisons	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Stump Present vs. Stump Absent	1	9.17	87.73	<.0001*
Partial vs. Intact & Stumphole	1	120	21.22	<.0001*
Intact Stump vs. Stumphole	1	109	3.95	0.049*

Animal-generated disturbances were consistently associated with stumps during the three-year study. In each census, stumps typically had 1-2 associated biopedturbations. Few animal disturbances occurred in areas without a stump (Figure 4.2). Based on mixed model analysis with LS Means comparisons, locations with a stump had significantly higher densities of animal disturbances each year than paired control areas without a stump. The type of stump also had a significant influence on frequency of biopedturbations. Partial stumps and stumpholes had more animal disturbances, especially in 2008 and 2009, than intact stumps (Figure 4.3).

Statistical analyses supported the differences among stump types. Mixed model analysis revealed a significant effect of stump type on density of animal-generated disturbances (Table 4.1). Year of sampling, canopy cover, and their interactions had no significant effect on density of animal disturbances. Orthogonal contrasts indicated a difference in animal disturbance densities associated with areas with and without, as well as the type of stump present (Table 4.2). The type of stump present influenced animal disturbance abundances, with differences between partially decomposed stumps compared to intact stumps and stumpholes. A significant difference in biopedturbations between intact stumps and stumpholes was also detected. Density of animal-generated disturbances surrounding more decomposed stumps supports previous studies on animal activity in pine savannas (Means 2006).

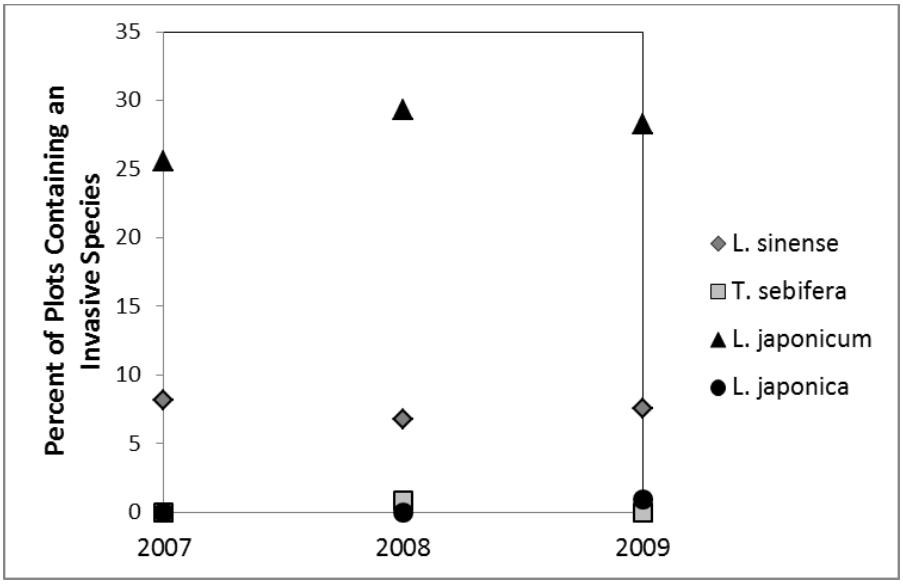

Figure 4.4. The percent of plots in pine savanna groundcover at Camp Whispering Pines that contained invasive species during the three-year study. Invasive species include *Ligustrum sinense* (Chinese privet), *Lonicera japonica* (Japanese honeysuckle), *Lygodium japonicum* (Japanese climbing fern), and *Triadica sebifera* (Chinese tallow tree).

Some invasive species have increased in occurrence in the longleaf pine savanna. Of the four invasive species present at Camp Whispering Pines, *L. japonicum* was the most abundant

and occurred most often in the study plots (Figure 4.4). The percent of plots containing *L. japonicum* was 3-4 times higher than the other three invasive species at Camp Whispering pines. Japanese climbing fern occurrence was also observed to slightly increase during the study, as documented in previous research (Chapter 2, Leichty et al. 2011a). I focused, therefore, on how disturbances influenced genet size (fronds/m^2) of *L. japonicum*.

The percentage of plots containing *L. japonicum* differed between open and closed canopy locations over the three-year study. Japanese climbing fern in open canopy areas increased over time, while plots containing the fern decreased in closed canopy locations (Figure 4.5). These results support the finding of previous research (Chapter 2), where occurrence of *L. japonicum* sharply increased in open canopy locations over a ten-year field study. Increased *L. japonicum* in open areas may reflect an association of local differences in fuels and variable fire effects, which are dependent on proximity to overstory pines.

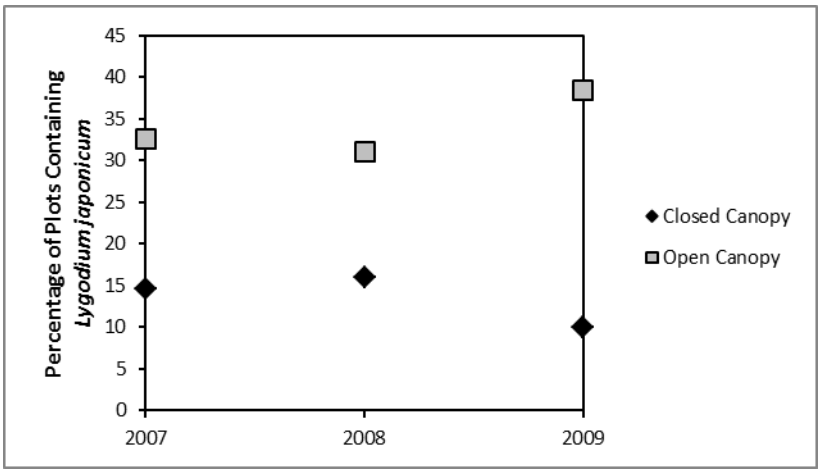

Figure 4.5. The proportion of plots in pine savanna groundcover at Camp Whispering Pines that contain *L. japonicum* in different canopy cover conditions during the three-year study.

Genet size of *L. japonicum* was influenced by presence of a stump and canopy condition. Figure 4.6 illustrates the average genet size of *L. japonicum* between stumps and similar areas

without stumps averaged over all three years. Fern genets were significantly larger in open canopy (20.67 ± 8.62) (mean ± s.e.) than in closed canopy (6.22 ± 1.16) for areas without stumps. Fern genets did not significantly differ for either closed (26.57 ± 4.67) or open canopy (12.22 ± 3.30) when a stump was present. Mixed model analysis indicated that the interaction between disturbance treatment (stump present or absent) and canopy cover condition had a significant effect on fern genet size (Table 4.3). Genets of *L. japonicum* were larger in open canopy with no stump, but larger under closed canopy with a stump. This suggests the presence of the stump may influence size of *L. japonicum* in different locations of the pine savanna.

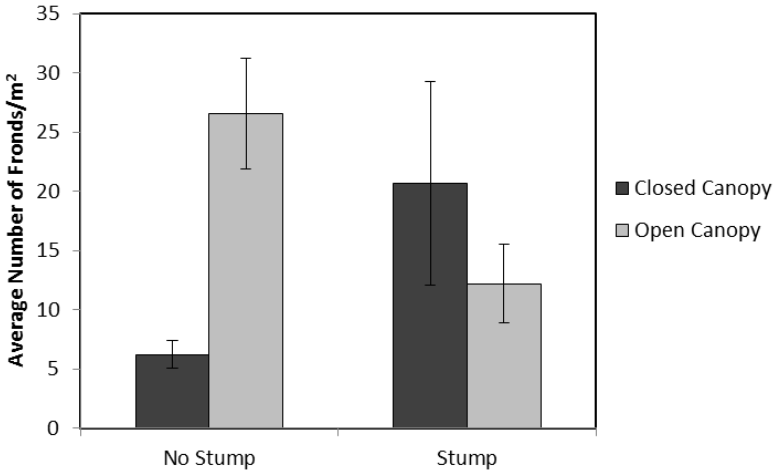

Figure 4.6. Comparison of genet size of Japanese climbing fern around stumps and in similar-sized paired areas without stumps under closed and open canopy at Camp Whispering Pines. Data were averaged over the three years sampled. Vertical bars represent mean ± one standard error.

Table 4.3. ANOVA table of the effects of disturbance treatment, canopy cover condition, year, and their interactions on genet size of *L. japonicum* at Camp Whispering Pines over the three-year study. Data were log transformed and analyzed with Proc Mixed procedure in SAS 9.1.3. Disturbance treatment denotes either stump present or stump absent. Canopy condition refers to open or closed canopy cover. Year refers to the year sampling of plots occurred (2007, 2008, 2009). Prescribed fire occurred in 2008. Non-fire years were 2007 and 2009. The AICC was 157.3 using CS covariance structure in the REPEATED statement. An asterisk (*) indicates significant effects.

Type 3 Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Disturbance Treatment	1	50	0.05	0.83
Canopy Condition	1	50	1.08	0.30
Disturbance Treatment*Canopy Condition	1	50	9.20	0.004*
Year	2	50	0.57	0.57
Disturbance Treatment*Year	2	50	0.83	0.44
Year*Canopy Condition	2	50	1.05	0.35
Year* Disturbance Treatment*Canopy Condition	2	50	0.30	0.74

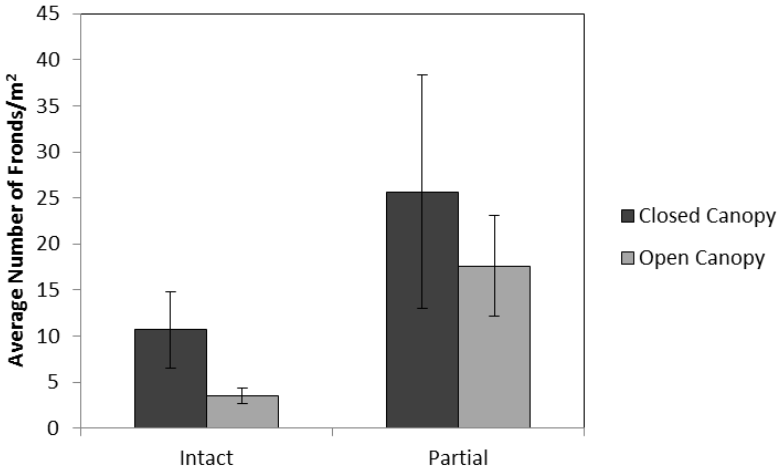

Figure 4.7. Comparison of Japanese climbing fern genet size for intact and partially decomposed stumps in areas of closed and open canopy at Camp Whispering Pines. Data were averaged over the three years sampled. Vertical bars represent mean $\pm$ one standard error.

Japanese climbing fern genet size was also influenced by the degree of stump decomposition. Figure 4.7 illustrates a significant difference in genet size between intact and partially decomposed stumps. Genets tend to be larger surrounding partial stumps than intact stumps. Mixed model analysis also supports a significant effect of stump type on genet size (Table 4.4). Based on these results, older, more decomposed stumps may be expected to have larger genets of *L. japonicum*.

Table 4.4. ANOVA table of the effects of stump type (intact stump, partial stump), canopy cover (open, closed), year (2007, 2008, 2009) and their interactions on genet size of *L. japonicum* at Camp Whispering Pines over the three-year study. Data were log transformed and analyzed using Proc Mixed procedure in SAS 9.1.3. The AICC was 288.1 using CS covariance structure in the REPEATED statement. An asterisk (*) denotes significant effects.

Type 3 Tests of Fixed Effects				
Effect	**Num DF**	**Den DF**	**F Value**	**Pr > F**
Stump Type	1	85	12.03	0.0008*
Canopy Condition	1	85	1.91	0.17
Stump Type*Canopy Condition	1	85	1.96	0.17
Year	2	85	0.17	0.85
Stump Type*Year	2	85	0.01	0.99
Year*Canopy Condition	2	85	1.32	0.27
Year*Stump Type*Canopy Condition	2	85	0.50	0.61

Discussion

Presence of a stump resulted in increased animal activity within a local area of the pine savanna. The study demonstrated that animal-generated disturbances occurred much more frequently around stumps than in neighboring locations without stumps. Stumps provide a source of shelter from extreme temperatures, fire, and predators, as well as a location for foraging in the longleaf pine savanna (Means 2006), where much of the ground surface is exposed. Other studies have indicated that animals in longleaf pine savannas utilized stumps, both that construct and do not construct independent burrows (Simkin et al. 2001, Simkin and Michener 2005, Means 2006). Burrowing organisms, such as gopher tortoises (*Gopherus polyphemus*), southeastern pocket gophers (*Geomys pinetis*), nine-banded armadillos (*Dasypus novemcinctus*), and cotton rats (*Sigmodon*) all have been observed excavating burrows in stump locations (Neill 1952, Simkin and Michener 2005, Means 2006). Once burrows are created and subterranean lateral roots exposed, other organisms, such as black racers (*Coluber constrictor*), fence lizards (*Sceloporus undulates*), and salamanders (Neill 1948, Platt 1999), eastern cottontails (*Sylvilagus*

floridanus) and bobwhite quail (*Colinus virginianus*) (Means 2006), utilize the burrows and exposed root cavities for refuge. These larger fauna have all been noted actively occupying burrows associated with stumps at Camp Whispering Pines. Arthropod fauna also play a significant role in soil disturbance surrounding stumps at Camp Whispering Pines. Wolf spiders (Lycosidae) have been observed constructing micro-burrows, while red-imported fire ants (*Solenopsis invicta*) have used the stump to support their mounds, possibly foraging on decomposers and termites within the sapwood. Several spiders, including wolf spiders (Lycosidae) and lynx spiders (Oxyopidae), have been observed ambushing prey at stump locations.

Animal biopedturbations were associated with particular stump types. The stump type is dependent on when the stump was created, the number of fires that have occurred, and the degree of decomposition. Intact stumps are likely recent in formation. Recently formed stumps would be expected to contain sapwood and this softer wood would be consumed by microarthropods, such as termites, and by decomposers, such as fungi and other microorganisms (Means 2006). Sapwood is a soft substrate that can be manipulated by organisms that forage on decomposers and microarthropods, resulting in additional wood and soil modification (Hermann 1993, Simkin and Michener 2005, Eldridge et al. 2009). Prevalence of microarthropods and microorganisms may attract other foraging animals, whereby leading to further manipulation of soil surrounding stumps. The length of time that sapwood remains present (and thus the stump is intact) should depend on effects of fires, which has been observed to consume sapwood readily under certain conditions (e.g., increased fuel accumulation, such as after hurricanes when fire intensity is elevated).

The longevity of stumps in longleaf pine savannas results from heartwood. Resin-soaked heartwood of longleaf pine, while very flammable when broken into smaller pieces, tends not to ignite as a unit when prescribed fires, like those at Camp Whispering Pines, move across the landscape. As a result, decomposition of stumps is slow; subterranean cavities of lateral roots and vertical integrity of the stump base persist for years (Mitchell et al. 2009). Typically, the stump fragments over time; the stump eventually burns in a fire, generating a stumphole that fills in gradually. Increased density of animal-generated disturbances surrounding partial stumps and stumpholes may be attributed to easier soil manipulation or exposed subterranean cavities for refuge. Additionally, partial locations may have more visible soil modification by larger fauna because of size and longevity of burrows and root cavities. Decreased animal activity in areas without stumps may be a response to exposure to predators or the absence of prey in some cases. With greater occurrence of fire, soil surrounding partial stumps may weaken, becoming an easier substrate for burrowing organisms to manipulate and form burrow refuges.

Secondary disturbances, in association with windstorms, may provide a window of opportunity for invasion. Hurricanes influence forest structure and composition in the pine savanna (Platt and Rathbun 1993, Turner et al. 1997, Beckage et al. 2006) by significantly altering canopy cover (Platt et al. 2000, Gilliam et al. 2006), and stand density (Turner et al. 1997) through defoliation, de-branching, and uprooting. Opening in the canopy results in heterogeneous light levels reaching the understory, as well as variation in fuel accumulation in localized areas (Platt and Rathbun 1993, Platt et al. 2006, Fahey and Puettmann 2007, Rich et al. 2007). The extent of canopy gaps translates into various responses of understory plant species within the immediate vicinity. For instance, increased light availability may result in increased herbaceous seedling recruitment (Brewer 1999a, b). The creation of a stump starts with a

windstorm that snaps a tree, creates a gap in the immediate canopy and produces a microsite favorable for colonization by plant species (Lee and Sturgess 2002). Opportunity for colonization at these stump microsites may be ephemeral (Setterfield et al. 2005), with increased competition occurring from surrounding understory species and seed bank reserves. Increased resource availability following windstorm disturbances could provide opportunity for invasive species colonization (Shea and Chesson 2002).

Canopy cover affects *L. japonicum* genet size and may enhance fern invasion. The success of *L. japonicum* may be correlated with time and extent of windstorm disturbance (Higgins and Richardson 1998, Shea and Chesson 2002, Shea et al. 2004); size of canopy gaps and increased light availability reaching ground level may be a strong determinate of *L. japonicum* success. While *L. japonicum* was present under both canopy cover conditions, fern occurrence was greater in open canopy. Canopy cover may influence fuel accumulation, with more fine fuels in areas with closed canopy compared to open canopy locations (Chapter 2, Thaxton and Platt 2006). Open canopy may have less fuel accumulation, which may translate to shortened duration of heating and lower total heat release (Chapter 2). Lower total heat released may reduce damage to belowground rhizomes and encourage *L. japonicum* emergence and spread post-fire. If conditions are favorable for colonization and establishment post-fire, *L. japonicum* spores could germinate, form mature sporophytes, and establish subterranean rhizomes enabling ferns to persist through subsequent fires (Chapter 2, Ranal 2003). Success of *L. japonicum* invasion may reflect the importance of the interaction between traits of the invasive plant and the environment in which the disturbance occurs (Higgins and Richardson 1998, Daehler 2003).

Presence of a stump influences genet size of *L. japonicum*, though it is dependent on canopy cover. When no stump was present, genet size of *L. japonicum* was larger in open canopy than closed canopy locations. When a stump was present, the relationship was reversed, with genet sizes larger in closed canopy locations. This difference in genet size may reflect differences in fuel accumulation and fire behavior. Less fuel accumulation is expected in open canopy compared to closed canopy as a function of distance from overstory pine trees (Chapter 2, Thaxton and Platt 2006). Larger genets are, therefore, anticipated in the open canopy, where less total heat would be released and fire would spread uninterrupted in the understory (Chapter 2). The presence of a stump, however, may act as a fire block, impeding fire spread. Further, moisture content of stumps may be influenced by canopy cover, with increased retention of moisture under closed canopy. Stumps in open canopy locations would be expected to have decreased moisture content potentially as a result of increased light availability. The combination of fuel accumulation and distribution with moisture content may affect heat released, thus influencing *L. japonicum* emergence in a local area.

Degree of stump decomposition influenced Japanese climbing fern genet size. Intact stumps in open canopy had smaller genets than partially decomposed stumps. The difference in genet size may be an effect of stump age. Recently formed stumps are expected to contain more sapwood, which can combust and burn readily during a fire, compared to partial stumps that are primarily composed of heartwood (Means 2006). Greater heat released would be expected surrounding intact stumps, thus resulting in smaller *L. japonicum* genets. Hot-spots of Japanese climbing fern invasion should, therefore, be anticipated surrounding partially decomposed stumps where fire severity is reduced.

Some disturbances are beneficial to invasion. Disturbances have been cited to facilitate and promote invasion through increased resources availability and decreased competition from native species (Hobbs and Huenneke 1992, Mack and D'Antonio 1998, Mack et al. 2000, D'Antonio and Meyerson 2002, Lockwood et al. 2007). Japanese climbing fern may invade a new location via copious amounts of wind-dispersed spores (Munger 2005, Van Loan 2006b, Mehltreter et al. 2010, Minogue et al. 2010), which land on moist, exposed soil, germinate, and produce mature sporophytes (Van Loan 2006a). Formation of mature sporophytes leads to establishment and expansion of shallow subterranean rhizomes (Clarke 1936, Mueller 1982, Leichty et al. 2011a). Proportion of plots containing *L. japonicum* was greater in areas of open canopy, though only in areas without a stump. This suggests that open canopy locations without a stump may be more easily colonized. Once the fern establishes, however, *L. japonicum* can persist in locations regardless of canopy cover or presence of stump disturbance.

Windstorms create conditions that benefit both animals and *L. japonicum*, but for different reasons. Stumps created by tree falls are important microsites for animal activities, including accessible refuge. Canopy openings from tree falls increase light levels in the understory, stimulating fern growth. The occurrence of biopedturbation does not, however, appear to enhance or hinder *L. japonicum* spread in the longleaf pine savanna. Soil manipulation may have a neutral effect on *L. japonicum* spread because of fern growth and reproductive characteristics. Some ferns species (e.g., *Pteridium* aquilinum) are capable of survival in the spore bank (Fletcher and Kirkwood 1979, Dyer and Lindsay 1992). Japanese climbing fern may persist in the spore bank, withstanding burial of spores by biopedturbations until conditions are favorable for germination. New colonization of *L. japonicum* may be more successful in areas of opened canopy following a fire in pine savannas, during ephemeral increased light availability. If

L. japonicum successfully establishes rhizomes, the likelihood of surviving subsequent fires would be expected to increase. Unlike other studies that have demonstrated promotion or suppression of exotic species invasion by small-scale animal disturbances (Eldridge et al. 2009, Mazía et al. 2010, Otfinowski and Kenkel 2010), windstorms appear to be the dominant disturbance, providing a mechanism necessary for *L. japonicum* spread in longleaf pine savannas.

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Chapter 5

Conclusions

General Implications

The studies within this dissertation contribute to the basic knowledge of disturbance-dependent longleaf pine savannas by exploring how prescribed fire, previous windstorm disturbances, and biopedturbations influence the invasion of *Lygodium japonicum* and native species composition. The spread of *L. japonicum* was described through exploring how the proportion of plots containing the fern increased over time within the pine savanna. The different disturbances operating in the pine savanna, and how they influence environmental aspects, were used to assess whether *L. japonicum* is malignant and outcompeting native species or somewhat benign and becoming a member of the groundcover flora. Determining how *L. japonicum* and native species are influenced by disturbances can aid in better restoration of imperiled longleaf pine savannas. This dissertation supports the role of fire creating heterogeneous patches at ground level, which influence native species composition and *L. japonicum* (Chapter 2 and 3). The dissertation additionally addresses how different disturbances may facilitate or suppress invasion (Chapter 2 and Chapter 4).

Five main ideas were developed based on how disturbances influence groundcover vegetation. First, windstorms and fire generate heterogeneity in the understory, thus influencing native species composition and invasion of *L. japonicum* (Chapter 2, 3, and 4). Windstorms alter canopy cover and distribute fuels into the understory, which in turn are consumed at varying intensities by fire. Both windstorms and fires increase resources availability (e.g., light levels), reduce competition and open patches within the groundcover to invasion. Second, severity of fires in longleaf pine savannas has variable effects on species composition, though the influence is transient for both native species and *L. japonicum* (Chapter 2 and 3). Fuel load distributed during windstorms contributes to the heterogeneity of patches in the understory and may

influence invasion, spread and frond emergence in the post-fire environment. Distribution of fuels in the understory reflects the third point, in which fuel accumulation decreases as distance from overstory pines increases (Chapter 2). Fourth, particular growth characteristics are necessary for survival and persistence in disturbance-dependent ecosystems (Chapter 2, 3, and 4). Native species and *L. japonicum* possess growth and reproductive structures to survive large- and small-scale disturbances occurring in longleaf pine savannas. Lastly, not all disturbances promote or suppress invasion (Chapter 4). Japanese climbing fern neither increased nor decreased in areas of greater biopedturbation, but genets were larger in open canopy locations. The results from this dissertation indicate that the influence of combined disturbances may have variable effects on both native and invasive species composition in longleaf pine savannas.

Heterogeneity of Disturbances

Disturbances interact on multiple scales to shape the longleaf pine savanna. Fire and windstorms influence several hectares, whereas animal-generated disturbances influence more localized areas, typically a few square meters (Chapter 3, Hermann 1993, Platt 1999, Beckage et al. 2006, Hoctor et al. 2006, Means 2006). These disturbances also occur at different temporal scales and may alter the ecosystem and species composition of the longleaf pine savanna (White and Pickett 1985, Platt and Connell 2003).

Fire is the primary large-scale disturbance of longleaf pine savannas, with punctuated, infrequent windstorm events. This dissertation supported the findings of previous studies on how windstorms and fires interact; windstorms generate various fuel loads that are consumed by fire at various severities and produce heterogeneous patches within the understory (Myers and van Lear 1998, Provencher et al. 2001, Gilliam et al. 2006, Thaxton and Platt 2006, Liu et al. 2008, Sah et al. 2010). Heterogeneity of patches generated by large-scale disturbances is important for

resource opportunity and invasion potential. The combination of windstorms and fire in longleaf pine savannas affect resource availability for both native species (Chapter 3) and *L. japonicum* (Chapter 2 and 4). Canopy cover, influenced by windstorms, can result in an increase of *L. japonicum* density in open canopy locations where light availability is increased (Chapter 4). Fire severity, a function of fuel accumulation and distribution resulting from windstorms, influences how *L. japonicum* and native groundcover species respond in the post-fire environment. Previous studies have examined how patch types in pine savannas associated with trees (Platt et al. 1988b, Noel et al. 1998, Gilliam et al. 2006) are also associated with local differences in fuel and fire effects (Chapter 2, Thaxton and Platt 2006). Results from this dissertation support similar finding, where increased fuel accumulation occurring under overstory trees results in greater fire severity compared to areas away from pines. Fluctuation in patches generated by subsequent windstorms and fires may alter resource availability and fire severity, hence exposing different locations in the understory to invasion by *L. japonicum*.

Fire severity transiently affects species composition in pine savanna understory. Fire consumes fine fuels and aboveground biomass, opening space and increasing light penetration in the understory, thus providing opportunity for colonization, establishment or re-emergence by groundcover species (Chapter 3). Variation in fuel accumulation and distribution results in patches of high and low fire severity (Thaxton and Platt 2006). Locations of high fire severity may be ephemeral openings for invasive species colonization. In this dissertation, sensitivity to total heat released was exhibited by both native species, as well as *L. japonicum* (Chapter 2 and 3). High fire severity patches in the post-fire environment may allow *L. japonicum* spores access for colonization, which require sterile, moist soil for germination (Chapter 2). The effects of fire severity were transient for both native species and *L. japonicum*, suggesting that if *L. japonicum*

successfully establishes rhizomes, it may survive subsequent fires, even in areas likely to have high fire severity. Amount of fuel accumulation and how it is consumed during a fire is dependent on weather conditions that occur between windstorm and fire disturbances (Platt and Connell 2003). Because fuel load is directly associated with windstorms, severe windstorm events are more likely to generate greater fuel accumulation. If these windstorms are followed by drought conditions, subsequent fires may burn hotter with longer heating duration in locations of increased fuel load, than if a windstorm had not occurred. Previous disturbances may, therefore, influence how future disturbances affect recruitment opportunities for both native and invasive species (Sousa 1984, Molinos and Donohue 2010, Carvalho et al. 2012).

Growth characteristics are important for the survival and persistence of species inhabiting disturbance-dependent pine savannas. Variation of fire severity may promote plants with particular traits that aid in colonization and establishment within the post-fire environment (Bond and Keeley 2005). Plants with short life cycles, high seed production and the capability to attain a height that captures light resources may be more successful following fire (Grime 1977, Masocha et al. 2011). Plants surviving in high fire severity locations may tend to possess belowground perennating structures protected from heating. *Lygodium japonicum* was shown to withstand locations of variable fire severity at Camp Whispering Pines (Chapter 2). Additionally, some native species were more abundant in high fire severity locations (Chapter 3). Other plant species, such as *Vaccinium darrowii* and *Pteridium aquilinum*, have been cited for tolerating high fire severity based on growth characteristics (Page 1976, Flinn and Wein 1977, Menges and Kohfeldt 1995, Rull 1999) Extensive subterranean rhizome and root systems coupled with high propagule production may have aided in survival of these plants, even in areas of increased heat duration.

Fire influences animal abundances surrounding stumps. The presence of a stump contributes to the heterogeneity of pine savanna groundcover by acting as "hot-spots" for animal activity. Stumps provide shelter from extreme temperatures, refuge from predators and areas to forage (Hermann 1993, Means 2006). Stump composition consists of an outer layer of sapwood that is easily decomposed and an inner heartwood layer that may persist through successive fires. This differential decomposition may result in a prolonged, but nonpermanent localized site for biopedturbation because of changing soil conditions surrounding the stump. Animal-generated disturbances were associated with stumps rather than similar areas without stumps (Chapter 4). Further, biopedturbations were greater surrounding partially decomposed stumps. Increased soil manipulation was predicted to result in increased successful colonization and establishment of *L. japonicum*, as cited in other invasive species studies (D'Antonio and Meyerson 2002, Setterfield et al. 2005, Martinson et al. 2008) based on increased resource opportunity (Shea and Chesson 2002, Shea et al. 2004). The results of this dissertation, however, indicate that *L. japonicum* occurrence and genet size are not promoted or suppressed by biopedturbation (Chapter 4). Rather, windstorms and fire were the contributing factors of *L. japonicum* success. Success of *L. japonicum* seems tied to rhizome integrity (Chapter 1 and 3), though potential spore bank survival and ample spore production may also aid in persistence. The role of propagule pressure and the spore bank in *L. japonicum* survival remain to be explored in disturbance-dependent ecosystems.

Model of Invasion by *Lygodium japonicum*

Timing of disturbances may play an important role in recruitment opportunities for *L. japonicum* invasion. Invasion of *L. japonicum* is likely to occur after a windstorm disturbance, when canopy gaps are created, or post-fire, when aboveground biomass has been removed and

belowground structures weakened. At this time, competition for light resources is reduced and moisture content of soil is increased (Chapter 2 and 3). Success of colonization may increase dependent on previous disturbance events. For example, a hurricane that generates multiple canopy gaps and increases fuel accumulation is likely to enhance *L. japonicum* invasion. Invasion may further be enhanced if flammable fuels are dried by reduced rainfall prior to fire. The combination of severe hurricane, drought conditions, and fire may yield more groundcover patches where light availability is increased and high fire severity occurs. Increased fire severity is likely to not only damage, but kill existing plant species, thus reducing competition for establishing *L. japonicum* spores. If the wind-dispersed spores colonize into areas where soil has been cleared by fire, successful germination may occur shortly after initial rains. The establishment of subterranean rhizomes may further insure successful survival following subsequent fire and windstorm disturbances. Colonization of stumps or areas under longleaf pine (*Pinus palustris*) trees is likely to lead to low establishment success as a result of increased fire severity via greater fuel accumulation (Chapter 2 and 4). Canopy gaps in non-stump locations may provide favorable recruitment conditions in the post-fire environment because of reduced aboveground biomass and increased light availability at ground level. Once established in open canopy locations, spread into more closed canopy areas may be easier, especially in patches experiencing high fire severity. Invasion opportunity is expected to decline as time since fire and/or windstorm disturbance increases. New opportunity for invasion restarts with successive disturbance events.

Restoration of Longleaf (*Pinus palustris*) Pine Savannas

Fire is an essential tool for restoring longleaf pine savannas. In these fire-frequented ecosystems, prescribed fire is necessary for maintenance of rich native plant biodiversity (Peet

and Allard 1993, Glitzenstein et al. 2003, Platt et al. 2006, Walker and Silletti 2006, Mitchell et al. 2009). Without frequent fires, encroachment of woody species increases, followed by a decline in herbaceous plants (Platt 1999, Passmore 2005, Frost 2006, Peet 2006, Thaxton and Platt 2006). Fires occurring in longleaf pine savannas also benefit non-native species. This dissertation provides evidence for the mechanisms that enable *Lygodium japonicum* to invade and persist despite the use of fire designed to restore the longleaf pine savanna ecosystem.

The conundrum between managing for native plant species and controlling the spread of *L. japonicum* occurs when fire generates openings in the understory through consumption of flammable fuels. The studies within this dissertation showed increased occurrence and density of *L. japonicum* (Chapter 2) under typical prescribed fire conditions in a longleaf pine savanna. The heterogeneous nature of fire and fire severity, coupled with windstorm disturbances, indicate that continued invasion of *L. japonicum* is likely. With each disturbance type, recruitment opportunities exist, such as increased light levels and exposed soils. The studies within this dissertation indicate potential locations of the highest risk of invasion, such as open canopy areas immediately post-fire. While fire may benefit increased occurrence and density of *L. japonicum*, removal of fire is likely to negatively influence resiliency of the ecosystem (Liu et al. 2008) by reducing and/or damaging keystone structures (e.g., longleaf pine trees and bunchgrasses) (Tews et al. 2004).

The current prescribed fire regime alone may not be sufficient for control of *L. japonicum*. Studies have documented invasion of non-native plant species associated with prescribed fire (Pyke et al. 2010, Masocha et al. 2011). Current management techniques implemented at Camp Whispering Pines involve burning different fire blocks on biennial rotation. The burning practice yields burned and unburned patches within the larger landscape of

the camp and high native species biodiversity has been documented as a result (Platt et al. 2006, Myers and Harms 2009a). This prescribed burning method also results in continual *L. japonicum* spore invasion of burned locations from unburned areas, as well as regeneration of aboveground fronds from subterranean rhizomes. Alteration of prescribed burning, such as burning all fire blocks within the same year, could potentially minimize prevalence of *L. japonicum*, but may result in reduction of native groundcover. Reduction of *L. japonicum* may require manual removal of aboveground fronds prior to spore production to attempt to reduce total spore amount in the system. Also, application of herbicide into the rhizosphere to reduce vegetative expansion prior to fire may reduce post-fire emergence of fronds. (Pieterson et al. 2010). Determining the viability and persistence of both reproductive structures is important for directing control activities. Exploration of different control methods, based on *L. japonicum* reproduction and spread, is a necessary component of future longleaf pine restoration efforts.

Consideration of current and potential non-native species growth characteristics, as well as their likelihood of altering the disturbance regime, becomes a necessary study in fire-frequented ecosystems. For the longleaf pine savanna, some non-native species (e.g., *Imperata cylindrica*) may result in serious fire regime alteration (Jose et al. 2002, Miller 2007), while others may have little effect. Recognition of *L. japonicum* as a component of longleaf pine groundcover may be necessary to conserve the ecosystem as a whole.

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Appendix A: Photographs of Study Site

Figure A.1. Photograph of longleaf pine savanna at Camp Whispering Pines, Tangipahoa Parish, Independence, Louisiana.

Appendix B: Photographs of fire severity, fuel consumption, and vegetation response at Camp Whispering Pines

Figure B.1. Photograph of different fire severities possible during a prescribed fire at Camp Whispering Pines. Low-severity fire (A) can occur when fire moves across the surface consuming fuels, whereas higher severity fires (B) may result in locations of downed tree crowns and higher accumulation of fine-fuels, such as pine needles.

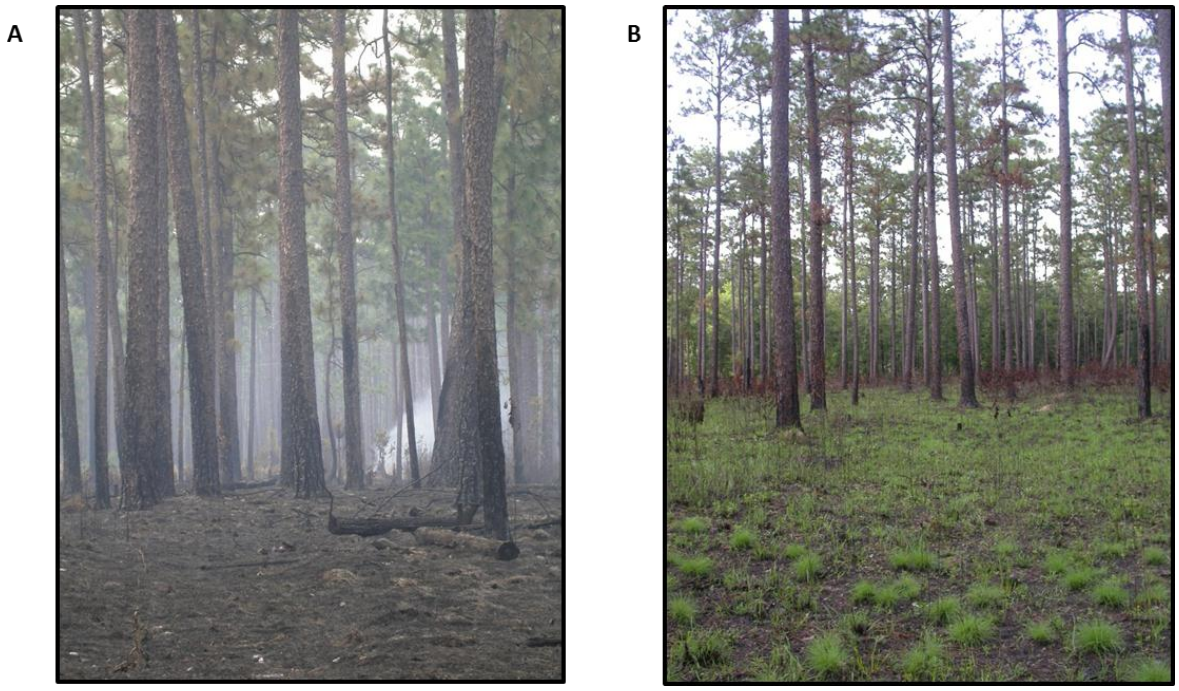

Figure B.2. Photograph illustrating fuel consumption during and vegetative return after recurrent low-intensity prescribed fires at Camp Whispering Pines. Low-intensity fires move over the ground surface (A), consuming fine-fuels and vegetation. The low-intensity fires stimulate regrowth and flowering of native vegetation (B), with vegetation returning approximately two weeks post-fire.

Appendix C: Fine-fuel Treatments

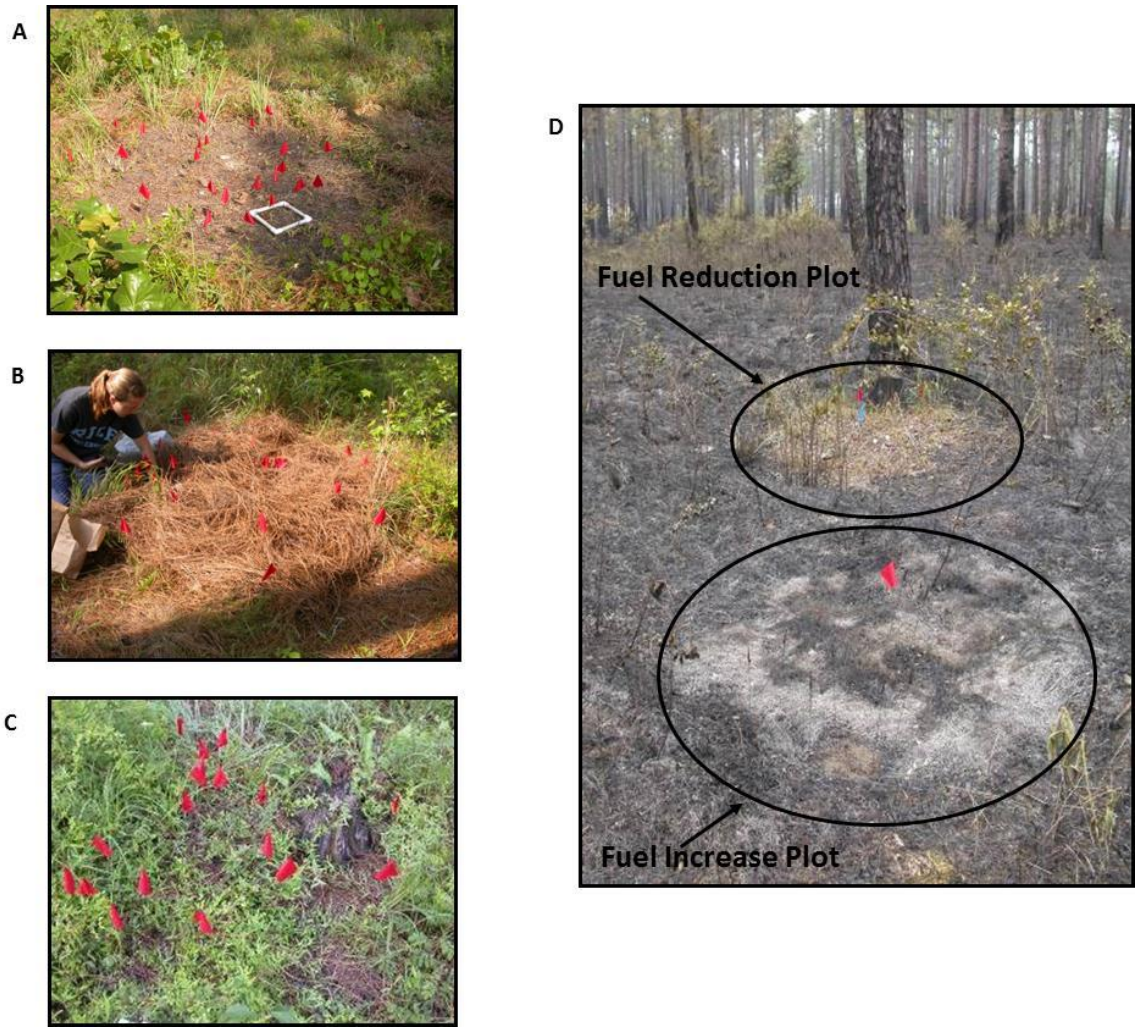

Figure C.1. Fine-fuel treatments pre- and post-fire at Camp Whispering Pines, Tangipahoa Parish, Louisiana. Fuel treatments (Reduction (A), Increase (B), and Unaltered (C)) were applied prior to May 2007 prescribed fires. Immediately post-fire (D) differences in fuel consumption between Reduction and Increase treatments were observed in the field.

Appendix D: Photographs of *Lygodium japonicum*

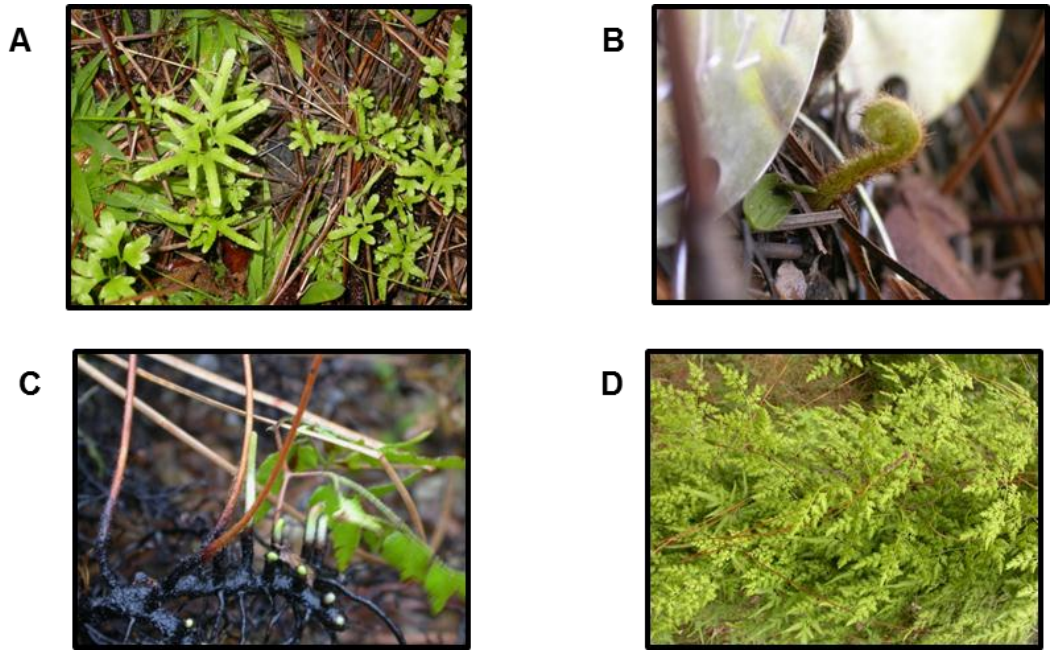

Figure D.1. *Lygodium japonicum* (A) young sporophytes, (B) emerging fiddlehead, (C) subterranean rhizomes, and (D) mass of twining fronds.

Appendix E: Photographs of Stump Classification Types

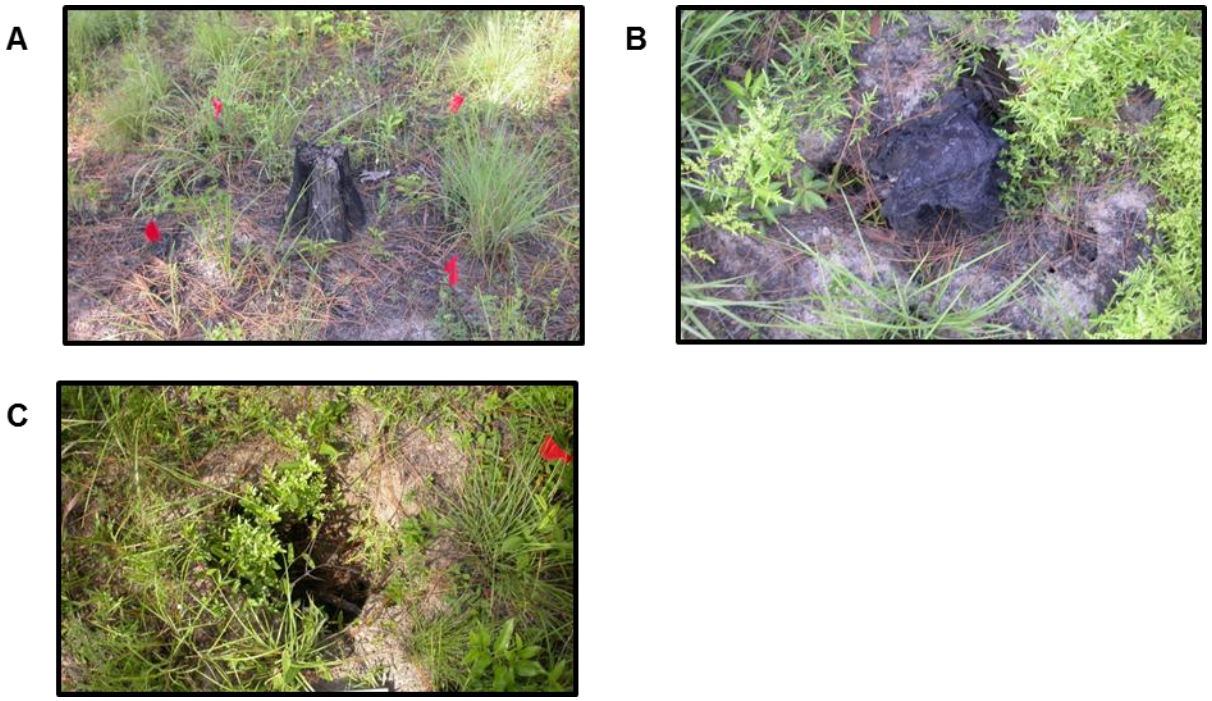

Figure E.1. Stump type classification based on degree of soil disruption (A) intact, (B) partially decomposed, and (C) completely formed stump hole.

Appendix F: Plant Species Classified and Identified For Chapter Three

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Euphorbiaceae	Acalypha	gracilens		A	Forb	Native
Asteraceae	Ageratina	aromatica		P	Forb	Native
Poaceae	Andropogon	virginicus	decipiens	P	Graminoid	Native
Poaceae	Aristida	purpurescens		P	Graminoid	Native
Asteraceae	Boltonia	diffusa		P	Forb	Native
Ophioglossaceae	Botrychium	biternatum		P	Fern	Native
Verbenaceae	Callicarpa	americana		P	Woody	Native
Bignoniaceae	Campsis	radicans		P	Vine	Native
Rhamnaceae	Ceanothus	americanus		P	Woody	Native
Fabaceae	Centrosema	virginianum		P	Forb	Native
Fabaceae	Chamaecrista	nictitans		P	Forb	Native
Asteraceae	Chaptalia	tomentosa		P	Forb	Native
Asteraceae	Chrysopsis	mariana		P	Forb	Native
Asteraceae	Cirsium	horridulum		A	Forb	Native
Fabaceae	Clitoria	mariana		P	Forb	Native
Asteraceae	Conoclinium	coelestinum		P	Forb	Native
Rosaceae	Crataegus	marshalii		P	Woody	Native
Fabaceae	Crotalaria	purshii		P	Forb	Native
Fabaceae	Desmodium	ciliare		P	Forb	Native
Fabaceae	Desmodium	lineatum		P	Forb	Native
Fabaceae	Desmodium	sp.		P	Forb	Native
Fabaceae	Desmodium	tenuifolium		P	Forb	Native
Poaceae	Dichanthelium	aciculare		AP	Graminoid	Native
Poaceae	Dichanthelium	aciculare	angustifolium	AP	Graminoid	Native
Poaceae	Dichanthelium	dichotomum	ensifolium	AP	Graminoid	Native
Poaceae	Dichanthelium	ovale		AP	Graminoid	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Poaceae	Dichanthelium	ravenelii		AP	Graminoid	Native
Poaceae	Dichanthelium	sp.		AP	Graminoid	Native
Poaceae	Dichanthelium	sphaerocarpon		AP	Graminoid	Native
Poaceae	Dichanthelium	strigosum		AP	Graminoid	Native
Poaceae	Dichanthelium	tenue		AP	Graminoid	Native
Rubiaceae	Diodia	sp.		AP	Forb	Native
Rubiaceae	Diodia	virginiana		AP	Forb	Native
Ebenaceae	Diospyros	virginiana		P	Woody	Native
Droseraceae	Drosera	brevifolia		AP	Forb	Native
Asteraceae	Elephantopus	tomentosus		P	Forb	Native
Poaceae	Eragrostis	spectabilis		P	Graminoid	Native
Asteraceae	Eupatorium	album		P	Forb	Native
Asteraceae	Eupatorium	rotundifolium		P	Forb	Native
Asteraceae	Eupatorium	semiserratum		P	Forb	Native
Euphorbiaceae	Euphorbia	corollata		P	Forb	Native
Euphorbiaceae	Euphorbia	sp.		P	Forb	Native
Asteraceae	Euthamia	leptocephala		P	Forb	Native
Fabaceae	Galactia	volubilis		P	Forb	Native
Rubiaceae	Galium	orizabense	laevicaule	P	Forb	Native
Rubiaceae	Galium	sp.		P	Forb	Native
Ericaceae	Gaylussacia	dumosa		P	Woody	Native
Gelsemiaceae	Gelsemium	sempervirens		AP	Vine	Native
Poaceae	Gymnopogon	brevifolius		P	Graminoid	Native
Rubiaceae	Hedyotis	procumbens		P	Forb	Native
Asteraceae	Helianthus	angustifolius		P	Forb	Native
Asteraceae	Helianthus	radula		P	Forb	Native
Malvaceae	Hibiscus	aculeatus		P	Forb	Native
Clusiaceae	Hypericum	crux-andreae		P	Woody	Native
Clusiaceae	Hypericum	sp.		P	Woody	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Clusiaceae	Hypericum	setosum		P	Woody	Native
Aquifoliaceae	Ilex	glabra		P	Woody	Native
Aquifoliaceae	Ilex	vomitoria		P	Forb	Native
Fabaceae	Lespedeza	capitata		P	Forb	Native
Fabaceae	Lespedeza	repens		P	Forb	Native
Asteraceae	Liatris	squarrulosa		P	Forb	Native
Oleaceae	Ligustrum	sinense		P	Woody	Invasive
Hamamelidaceae	Liquidambar	styraciflua		P	Woody	Native
Campanulaceae	Lobelia	puberula		P	Forb	Native
Schizaeaceae	Lygodium	japonicum		P	Fern	Invasive
Fabaceae	Mimosa	microphylla		P	Forb	Native
Fabaceae	Mimosa	strigillosa		P	Forb	Native
Loganiaceae	Mitreola	sessilifolia		A	Forb	Native
Oxalidaceae	Oxalis	stricta		P	Forb	Native
Poaceae	Panicum	anceps		P	Graminoid	Native
Poaceae	Panicum	verrucosum		A	Graminoid	Native
Poaceae	Panicum	virgatum		P	Graminoid	Native
Passifloraceae	Passiflora	lutea		P	Forb	Native
Polemoniaceae	Phlox	divaricata		P	Forb	Native
Euphorbiaceae	Phyllanthus	caroliniensis		A	Forb	Native
Pinaceae	Pinus	palustris		P	Woody	Native
Pinaceae	Pinus	taeda		P	Woody	Native
Asteraceae	Pityopsis	graminifolia		P	Forb	Native
Rosaceae	Prunus	serotina		P	Woody	Native
Pteridiaceae	Pteridium	aquilinum		P	Fern	Native
Lamiaceae	Pycnanthemum	albescens		P	Forb	Native
Lamiaceae	Pycnanthemum	tenuifolium		P	Forb	Native
Fagaceae	Quercus	niga		P	Woody	Native
Fagaceae	Quercus	marilandica		P	Woody	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Anacardiaceae	Rhus	copallinum		P	Woody	Native
Fabaceae	Rhynchosia	reniformis		P	Forb	Native
Cyperaceae	Rhynchospora	ciliaris		P	Graminoid	Native
Rosaceae	Rubus	cuneifolius		P	Vine	Native
Rosaceae	Rubus	trivialis		P	Vine	Native
Asteraceae	Rudbeckia	hirta		P	Forb	Native
Acanthaceae	Ruellia	caroliniensis		P	Forb	Native
Acanthaceae	Ruellia	sp.		P	Forb	Native
Lauraceae	Sassafras	albidum		P	Woody	Native
Poaceae	Schizachyrium	scoparium		P	Graminoid	Native
Poaceae	Schizachyrium	tenerum		P	Graminoid	Native
Cyperaceae	Scleria	ciliata	ciliata	P	Graminoid	Native
Cyperaceae	Scleria	pauciflora		P	Graminoid	Native
Lamiaceae	Scutellaria	integrifolia		P	Forb	Native
Smilacaceae	Smilax	bona-nox		P	Vine	Native
Smilacaceae	Smilax	glauca		P	Vine	Native
Smilacaceae	Smilax	rotundifolia		P	Vine	Native
Smilacaceae	Smilax	smallii		P	Vine	Native
Solanaceae	Solanum	carolinense		P	Forb	Native
Asteraceae	Solidago	odora		P	Forb	Native
Asteraceae	Solidago	rugosa		P	Forb	Native
Fabaceae	Stylosanthes	biflora		P	Forb	Native
Asteraceae	Symphyotrichum	adnatum		P	Forb	Native
Asteraceae	Symphyotrichum	dumosum		P	Forb	Native
Asteraceae	Symphyotrichum	patens		P	Forb	Native
Fabaceae	Tephrosia	floridana		P	Forb	Native
Fabaceae	Tephrosia	spicata		P	Forb	Native
Apocynaceae	Trachelospermum	difforme		P	Forb	Native
Euphorbiaceae	Tragia	smallii		P	Forb	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
	Unknown	Sedge			Graminoid	Native
Asteraceae	unknown Aster				Forb	Native
Asteraceae	Unknown Aster 601				Forb	Native
	Unknown Graminoid 424				Graminoid	Native
	Unknown Graminoid 431				Graminoid	Native
	Unknown Forb 250				Forb	Native
	Unknown Forb 304				Forb	Native
	Unknown Forb 305				Forb	Native
	Unknown Forb 306				Forb	Native
	Unknown Forb 311				Forb	Native
	Unknown Forb 400				Forb	Native
	Unknown Forb 401				Forb	Native
	Unknown Forb 403				Forb	Native
	Unknown Forb 404				Forb	Native
	Unknown Forb 407				Forb	Native
	Unknown Forb 409				Forb	Native
	Unknown Forb 413				Forb	Native
	Unknown Forb 423				Forb	Native
	Unknown Forb 425				Forb	Native
	Unknown Forb 428				Forb	Native
	Unknown Forb 618				Forb	Native
	Unknown Forb Fine				Forb	Native
	Unknown Forb Purple flower				Forb	Native
	Unknown Mint 411				Forb	Native
	Unknown Mint 428				Forb	Native
Ericaceae	Vaccinium	arboreum		P	Woody	Native
Ericaceae	Vaccinium	darrowii		P	Woody	Native
Ericaceae	Vaccinium	elliotii		P	Woody	Native
Ericaceae	Vaccinium	sp.		P	Woody	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Ericaceae	Vaccinium	stamineum		P	Woody	Native
Violaceae	Viola	primulifolia		P	Forb	Native
Violaceae	Viola	septemloba		P	Forb	Native

Appendix G: Plant Species Classified and Identified For Chapter Four

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Euphorbiaceae	Acalypha	gracilens		A	Forb	Native
Sapindaceae	Acer	rubrum		P	Woody	Native
Asteraceae	Ageratina	aromatica		P	Forb	Native
Poaceae	Andropogon	capillipes		P	Graminoid	Native
Poaceae	Andropogon	gerardii		P	Graminoid	Native
Poaceae	Andropogon	sp		P	Graminoid	Native
Poaceae	Andropogon	virginicus	decipiens	P	Graminoid	Native
Poaceae	Aristida	purpurescens		P	Graminoid	Native
Asclepiadaceae	Asclepias	connivens		P	Forb	Native
Asteraceae	Boltonia	diffusa		P	Forb	Native
Ophioglossaceae	Botrychium	biternatum		P	Fern	Native
Verbenaceae	Callicarpa	americana		P	Woody	Native
Bignoniaceae	Campsis	radicans		P	Vine	Native
Asteraceae	Carphephorus	odoratissimus		P	Woody	Native
Juglandaceae	Carya	texana		P	Woody	Native
Rhamnaceae	Ceanothus	americanus		P	Woody	Native
Fabaceae	Centrosema	virginianum		P	Vine	Native
Fabaceae	Chamaechrista	nictitans		P	Forb	Native
Asteraceae	Chaptalia	tomentosa		P	Forb	Native
Poaceae	Chasmanthium	laxum		P	Graminoid	Native
Asteraceae	Chrysopsis	mariana		P	Forb	Native
Asteraceae	Cirsium	horridulum		A	Forb	Native
Fabaceae	Clitoria	mariana		P	Forb	Native
Asteraceae	Conoclinium	coelestinum		P	Forb	Native
Rosaceae	Crataegus	marshalii		P	Woody	Native
Fabaceae	Crotalaria	purshii		P	Forb	Native
Euphorbiaceae	Croton	glandulosus		A	Forb	Native
Fabaceae	Desmodium	ciliare		P	Forb	Native
Fabaceae	Desmodium	lineatum		P	Forb	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Fabaceae	Desmodium	marilandicum		P	Forb	Native
Poaceae	Dichanthelium	aciculare		AP	Graminoid	Native
Poaceae	Dichanthelium	aciculare	angustifolium	AP	Graminoid	Native
Poaceae	Dichanthelium	dichotomum	ensifolium	AP	Graminoid	Native
Poaceae	Dichanthelium	laxiflorum		AP	Graminoid	Native
Poaceae	Dichanthelium	ovale		AP	Graminoid	Native
Poaceae	Dichanthelium	ravenelii		AP	Graminoid	Native
Poaceae	Dichanthelium	sp.		AP	Graminoid	Native
Poaceae	Dichanthelium	sphaerocarpon		AP	Graminoid	Native
Poaceae	Dichanthelium	strigosum		AP	Graminoid	Native
Poaceae	Dichanthelium	tenue		AP	Graminoid	Native
Poaceae	Digitaria	filiformis		A	Graminoid	Native
Rubiaceae	Diodia	teres		AP	Forb	Native
Rubiaceae	Diodia	virginiana		AP	Forb	Native
Ebenaceae	Diospyros	virginiana		P	Woody	Native
Droseraceae	Drosera	brevifolia		AP	Forb	Native
Asteraceae	Elephantopus	elatus		P	Forb	Native
Asteraceae	Elephantopus	tomentosus		P	Forb	Native
Poaceae	Eragrostis	spectabilis		P	Graminoid	Native
Asteraceae	Eupatorium	album		P	Forb	Native
Asteraceae	Eupatorium	rotundifolium		P	Forb	Native
Asteraceae	Eupatorium	semiserratum		P	Forb	Native
Asteraceae	Eupatorium	sp.		P	Forb	Native
Euphorbiaceae	Euphorbia	corollata		P	Forb	Native
Euphorbiaceae	Euphorbia	sp.		P	Forb	Native
Asteraceae	Euthamia	caroliniana		P	Forb	Native
Asteraceae	Euthamia	letocephala		P	Forb	Native
Fabaceae	Galactia	volubilis		P	Forb	Native
Rubiaceae	Galium	orizabense	laevicaule	P	Forb	Native
Ericaceae	Gaylussacia	dumosa		P	Woody	Native
Gelsemiaceae	Gelsemium	sempervirens		AP	Vine	Native
Poaceae	Gymnopogon	brevifolius		P	Graminoid	Native
Rubiaceae	Hedyotis	procumbens		P	Forb	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Cistaceae	Helianthemum	carolinianum		P	Forb	Native
Asteraceae	Helianthus	hirsutus		P	Forb	Native
Asteraceae	Helianthus	radula		P	Forb	Native
Malvaceae	Hibiscus	aculeatus		P	Forb	Native
Asteraceae	Hieracium	gronovii		P	Forb	Native
Clusiaceae	Hypericum	crux-andreae		P	Forb	Native
Clusiaceae	Hypericum	hypericoides		P	Forb	Native
Clusiaceae	Hypericum	setosum		P	Forb	Native
Clusiaceae	Hypericum	sp.		P	Forb	Native
Lamiaceae	Hyptis	alata		P	Forb	Native
Aquifoliaceae	Ilex	glabra		P	Woody	Native
Aquifoliaceae	Ilex	vomitoria		P	Woody	Native
Fabaceae	Lespedeza	sp.		P	Forb	Native
Fabaceae	Lespedeza	capitata		P	Forb	Native
Fabaceae	Lespedeza	repens		P	Forb	Native
Asteraceae	Liatris	squarrulosa		P	Forb	Native
Oleaceae	Ligustrum	sinense		P	Woody	Invasive
Hamamelidaceae	Liquidambar	styraciflua		P	Woody	Native
Campanulaceae	Lobelia	brevifolia		P	Forb	Native
Campanulaceae	Lobelia	puberula		P	Forb	Native
Caprifoliaceae	Lonicera	japonica		P	Vine	Invasive
Schizaeaceae	Lygodium	japonicum		P	Fern	Invasive
Rubiaceae	Mitchella	repens		P	Forb	Native
Loganiaceae	Mitreola	petiolata		A	Forb	Native
Loganiaceae	Mitreola	sessilifolia		A	Forb	Native
Myricaceae	Morella	cerifera		P	Forb	Native
	moss					
Oxalidaceae	Oxalis	stricta		P	Forb	Native
Poaceae	Panicum	anceps		P	Graminoid	Native
Poaceae	Panicum	verrucosum		A	Graminoid	Native
Poaceae	Panicum	virgatum		P	Graminoid	Native
Poaceae	Paspalum	floridanum		P	Graminoid	Native
Poaceae	Paspalum	notatum		P	Graminoid	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Poaceae	Paspalum	sp.		P	Graminoid	Native
Passifloraceae	Passiflora	lutea		P	Forb	Native
Polemoniaceae	Phlox	sp.		P	Forb	Native
Euphorbiaceae	Phyllanthus	caroliniensis		A	Forb	Native
Pinaceae	Pinus	palustris		P	Woody	Native
Pinaceae	Pinus	taeda		P	Woody	Native
Asteraceae	Pityopsis	graminifolia		P	Forb	Native
Polygonaceae	Polygala	nana		A	Forb	Native
Rosaceae	Prunus	serotina		P	Woody	Native
Pteridiaceae	Pteridium	aquilinum		P	Fern	Native
Lamiaceae	Pycnanthemum	albescens		P	Forb	Native
Lamiaceae	Pycnanthemum	tenuifolium		P	Forb	Native
Fagaceae	Quercus	falcata		P	Woody	Native
Fagaceae	Quercus	hemisphaerica		P	Woody	Native
Fagaceae	Quercus	nigra		P	Woody	Native
Fagaceae	Quercus	sp.		P	Woody	Native
Fagaceae	Quercus	virginiana		P	Woody	Native
Melastomatoceae	Rhexia	mariana		P	Forb	Native
Anacardiaceae	Rhus	copallinum		P	Woody	Native
Fabaceae	Rhynchosia	reniformis		P	Forb	Native
Cyperaceae	Rhynchospora	ciliaris		P	Graminoid	Native
Rosaceae	Rubus	trivialis		P	Vine	Native
Asteraceae	Rudbeckia	hirta		P	Forb	Native
Acanthaceae	Ruellia	caroliniensis		P	Forb	Native
Acanthaceae	Ruellia	ciliosa		P	Forb	Native
Acanthaceae	Ruellia	pedunculata		P	Forb	Native
Acanthaceae	Ruellia	sp.		P	Forb	Native
Cyperaceae	Rush	sp.		P	Graminoid	Native
Lauraceae	Sassafras	albidum		P	Woody	Native
Poaceae	Schizachyrium	scoparium		P	Graminoid	Native
Poaceae	Schizachyrium	tenerum		P	Graminoid	Native
Cyperaceae	Scleria	ciliata	ciliata	P	Graminoid	Native
Cyperaceae	Scleria	pauciflora		P	Graminoid	Native

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
Lamiaceae	Scutellaria	integrifolia		P	Forb	Native
Smilacaceae	Smilax	glauca		P	Vine	Native
Smilacaceae	Smilax	pumila		P	Vine	Native
Smilacaceae	Smilax	rotundifolia		P	Vine	Native
Smilacaceae	Smilax	smallii		P	Vine	Native
Solanaceae	Solanum	carolinense		P	Forb	Native
Asteraceae	Solidago	odora		P	Forb	Native
Asteraceae	Solidago	rugosa		P	Forb	Native
Poaceae	Sporobolus	compositus	macer	P	Graminoid	Native
Poaceae	Sporobolus	sp.		P	Graminoid	Native
Fabaceae	Stylosanthes	biflora		P	Forb	Native
Asteraceae	Symphyotrichum	adnatum		P	Forb	Native
Asteraceae	Symphyotrichum	dumosum		P	Forb	Native
Asteraceae	Symphyotrichum	patens		P	Forb	Native
Asteraceae	Symphyotrichum	sp.		P	Forb	Native
Asteraceae	Taraxacum	sp.		P	Forb	Native
Fabaceae	Tephrosia	floridana		P	Forb	Native
Fabaceae	Tephrosia	spicata		P	Forb	Native
Anacardiaceae	Toxicodendron	radicans		P	Vine	Native
Apocynaceae	Trachelospermum	difforme		P	Forb	Native
Euphorbiaceae	Tragia	smallii		P	Forb	Native
Euphorbiaceae	Triadica	sebifera		P	Woody	Invasive
	Unknown 115				Unknown	
	Unknown 12				Unknown	
	Unknown 125				Unknown	
	Unknown 27				Unknown	
	Unknown 41				Unknown	
	Unknown 54				Unknown	
	Unknown 82				Unknown	
	Unknown 83				Unknown	
	Unknown Forb 156				Forb	
	Unknown Forb 158				Forb	
	Unknown Forb 441				Forb	

Family	Genus	Species	Var	Life Cycle	Plant Type	Origin
	Unknown Forb 521				Forb	
	Unknown Forb 616				Forb	
	Unknown Forb 623				Forb	
Cyperaceae	Unknown Sedge			P	Graminoid	Native
	Unknown Woody 1				Woody	
Ericaceae	Vaccinium	arboreum		P	Woody	Native
Ericaceae	Vaccinium	elliotii		P	Woody	Native
Ericaceae	Vaccinium	stamineum		P	Woody	Native
Caprifoliaceae	Viburnum	dentatum		P	Woody	Native
Violaceae	Viola	primulifola		P	Forb	Native
Violaceae	Viola	septemloba		P	Forb	Native
Vitaceae	Vitis	rotundifolia		P	Forb	Native

Vita

Becky J. Carmichael was born in Indiana to John and Mary Carmichael. She received her bachelor's degree in biological sciences from Purdue University in 1999. After graduation, Becky began a Student Conservation Association volunteer position at Shenandoah National Park, Luray, Virginia, where she worked as an interpretation ranger, developing and presenting programs about the natural history of the park to visitors of all ages. Becky continued to work with the National Park Service as a biological science technician at Joshua Tree National Park, Twenty-nine Palms, California, where she helped organize native plant salvaging projects and invasive species removal. Becky returned to Shenandoah National Park in 2001 as a biological science technician responsible for vegetation mapping to develop fire behavior models. In 2002, She worked briefly with the Indiana Department of Natural Resources. Becky began her doctoral studies at Louisiana State University in 2004 under the supervision of Dr. William J. Platt. Currently, Becky is a candidate for the Doctor of Philosophy degree and will graduate in May 2012.